

On the Classification of Actiniaria.

Part I.—Forms with Acontia and Forms with a Mesogloœal Sphincter.

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With Plate 22 and 32 Text-figures.

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I. INTRODUCTION.

WHILST working out recently the species contained in two collections of Actiniaria (the "Terra Nova" collection (79)¹

¹ Numbers in brackets refer to papers in the list of literature on pp. 564-572.

and one made by the Irish Fisheries Department (80)), I have been led to develop certain views on Actinian classification. Some of the families of Actiniaria are defined by only a small number of the more important characters possessed by the contained forms, with the result that some of them (e. g. Ilyanthidæ, Sagartiidæ, Paractidæ) represent not so much families as series of forms, each series including a number of animals which differ among themselves in ways so important as to be fundamental, although presenting a few common features. This arrangement neither represents the natural affinities of the genera nor does it throw much light upon their evolutionary history. It is often difficult also to allocate new species and genera to their correct position, because in a good many cases sufficiently precise generic definitions have not been arrived at. I have therefore thought it would be the best thing to set out for what they are worth the ideas I have developed during the course of my work. I have as yet applied them in detail to only one particular portion of the Actiniaria, and that application constitutes the following paper. I have begun with the group of forms belonging to the Actiniina which possess acontia or mesoglœal sphincters, because the collections I have been working at happened to present a preponderance of those forms; I am also well acquainted with some living members of it. I am hoping in due course to work out schemes on similar lines for the classification of those Actiniina not included in the present paper and of the Stichodactylina. As yet, however, I have made only a beginning on the two latter groups, so am publishing the finished section at once. More work on these two groups may throw fresh light on various Actinian problems, but is not very likely, I think, to affect the section dealt with in this paper to any extent.

With regard to the principles upon which my classification is based, I am glad to acknowledge my indebtedness to a paper which appeared last year on the question of the systematic position of the Phelliidæ, by Prof. G. C. Bourne (10),

and which has helped me greatly. I had, however, begun to work out the main ideas involved and to form my families in detail before I knew of Prof. Bourne's paper with its similar ideas.

I should like to record my most hearty thanks to Prof. H. J. Fleure and Prof. G. C. Bourne for help very kindly rendered in different ways, and to Dr. N. Annandale for specimens of some of his Indian anemones.

At the end of the paper I have included a discussion on the relative merits and stability of a number of generic characters, together with new definitions of the genera contained in the group here treated. I have felt this justified by the difficulty I have had in identification and related matters, and have done it in the hope that identification may be rendered simpler by it. In any case it is a convenience to work with a collection of generic definitions, and in the end I hope to make it complete.

In the two reports on anemones already published I have used the ordinary classification almost as it stood because I had not at the time of writing them got far enough with any other scheme. For the purposes of this paper I am accepting provisionally the main division of the Actiniaria into Actiniina and Stichodactylina. As I have mentioned before (79, p. 14) I have felt unable to accept Carlgren's division of Actiniaria into Protantheæ and Nynantheæ, and in this I am following McMurrich, Haddon, Duerden and Bourne. The chief difference between these two tribes is that in the Protantheæ there is ectodermal longitudinal musculature in body-wall and actinopharynx, while in the Nynantheæ there is not. Gonactinia and Protanthea are the original Protantheæ. But if with them we are to include all forms possessing this ectodermal musculature, it will mean picking out a form here and there from widely different families and putting them together. The following forms are recorded as possessing the ectodermal musculature, though Carlgren has expressed doubts about it in the case of some of them (the list is not meant to be exhaustive, but merely gives a selection):

Protanthea.	Bunodeopsis spp.
Gonactinia.	Bolocera brevicornis
Corallimorphus.	(but not other Boloceras).
Corynactis.	
Thanmactis medusoides.	Aiptasia couchi.
Phymanthus crnifer.	Boloceroides.
Ricordea florida.	Actinotryx sanctithomae.
	Actinoporus elegans.

A more divergent collection could hardly be made. Apart from the ectodermal musculature, their other important characters show that they belong to totally different and unrelated families. The ectodermal musculature of the body-wall is no doubt the survival in a case here and there of a primitive character possessed by the original ancestor of the group and which has been lost in most cases. It is even possible that careful study of the life and habits of the forms possessing it would reveal a reason for its retention in each case. But to use it in classification leads to unnatural results.

There will be found below references to correlation between habit or life conditions and structure. I should like to make a plea for the study of living anemones and their life-habits wherever possible. As Annandale has remarked (4, p. 72), it is doubtful whether Gosse was so far from the truth as later systematists supposed when he laid stress upon the study of the living organism in the case of Actinians. At any rate, when one studies living species one seems to gather a much better idea of their relationships and of the meaning of their structure than if anatomy is exclusively relied upon. In the case of allied *species* distinction is sometimes extremely simple when they are alive, but very difficult, if not impossible, when dead, even with the aid of anatomy.

I ought to mention that in this paper I have not founded anything on incomplete descriptions or upon descriptions of doubtful species where that could be avoided. It seems unprofitable to build much upon species of which our knowledge may need revision. I have included in the lists of genera which

follow the family definitions at the end of the paper the names of a number of doubtful genera (in a separate list, in each case, from the better-known genera), but this is, of course, quite tentative.

In re-defining the genera I have been unable to avoid a certain amount of re-arrangement of species and splitting or fusing of genera. I have done my best to keep this within the narrowest possible limits, and have pointed out all changes made. Some such revision is bound to take place when all the genera are surveyed together, and it means that the definitions gain in precision and therefore render identification easier, and it has been my aim to express in them the natural relationships of the forms, and to apply similar principles all through, with exceptions in individual cases which seemed to call for special treatment. I may add that I have personal knowledge of living or preserved specimens, and in most cases of sections, of representatives of half the genera defined; in some cases I have added to generic definitions from my own study of the forms in question. My data about other forms are of course obtained from literature. In cases where there are only one or two species in a given genus, it is of course always possible that the addition of new species to the genus may necessitate alteration of minor points in the definition.

Finally, I have not meant the paper to be an exhaustive compilation as regards lists of species and synonymy. I have therefore included, for convenience, just such main synonyms as are strictly necessary. With regard to the lists of species following the genera, these are not in all cases complete; but as far as I know they include at any rate most of the species which have been investigated anatomically, except in one or two large genera.

I wish to acknowledge with thanks the permission to reprint some of the text-figures from other publications. Text-fig. 12 is reprinted from Prof. Bourne's paper on Phelliidae from New Guinea ('Quart. Journ. Micr. Sci.'), by kind permission of the author. Text-figs. 1, 22, 23 and 32

are reprinted from my "Terra Nova" report, *Actiniaria*. Text-figs. 24, 25, 27 and 31 are reprinted from my paper on Irish *Actiniaria* in 'Proc. R. I. Acad.' The other text-figures and the plates are freshly drawn for this paper.

II. BRIEF HISTORIES OF THE SAGARTIIDÆ AND PARACTIDÆ.

The brief histories which follow do not claim in any way to be complete. Their aim is to simply review the chief modifications undergone by the families since their inception, in such a way as to render the subsequent discussions intelligible. With that end in view I have thought it permissible to repeat a good deal which has been written by various authors, but which is scattered about in different papers.

SAGARTIIDÆ.

P. H. Gosse founded a family which he called "Sagartiadæ" in 1858 (P. p. 415) and defined it thus: "Sagartiadæ. Basis adhaerens. Tentacula simplicia, in cyclis continuis digesta. Cutis, pro filis retractilibus armatis emittendis, perforata." The genera included were *Actinoloba* and *Sagartia*. In his 'Actinologia Britannica,' p. 9, he gave a fuller English diagnosis, adding nothing essential to the preceding. The genera there included were *Actinoloba*, *Sagartia*, *Phellia*, *Adamsia*, *Gregoria*, *Discosoma*. *Sagartia* is of course the typical genus of the family, and both Gosse himself (37, p. 122) and Haddon later on (42, p. 302) have made it perfectly clear that the species regarded by the former, the founder of the genus, as the genotype, was *S. miniata*. Therefore it will be taken for granted throughout this paper that whatever may happen to the various genera under discussion, the name *Sagartiadæ* (in its amended form, *Sagartiidæ*) must be applied to the family containing *Sagartia* as typified by *S. miniata* and its immediate relatives.

In 1868 A. E. Verrill ('Proc. Essex Inst.,' vol. v) included

the Sagartids as a sub-family under the Actiniidæ. He placed *Phellia* in another sub-family, the *Phellinæ*, however.

In 1883 A. Andres included *Actinoloba*, *Heliactis*, *Cylistia*, *Adamsia*, *Aiptasia*, *Sagartia* and *Nemactis* in the *Sagartidæ*, excluding *Phellia* and *Gregoria*, placing the former in *Phellidæ* and not definitely classifying the latter.

In 1882 R. Hertwig endeavoured to establish the family on anatomical grounds. He was, however, unlucky. It so happened that the particular acontiated anemones dealt with in his investigations belonged to a portion of the family in which the members have strong mesoglœal sphincters, and have only six pairs of perfect mesenteries, which are sterile. Even the representative of the genus *Sagartia* which he had investigated (*S. parasitica*), happened to be the one species which had been included in that genus by mistake, and which he referred to its correct position in the genus *Calliactis*. The result of this was that Hertwig made a definition of the *Sagartidæ* which was based upon the presence of acontia, together with the other anatomical features above mentioned, *but which excluded Sagartia miniata and its allies, the true types of the family, from the Sagartidæ*.¹

In 1889 A. C. Haddon (42, pp. 301-305) referred to most of the foregoing facts, and showed that *Sagartia miniata* and others had more than six pairs of perfect mesenteries, thus differing from the forms described by Hertwig. Haddon considered that the time had not arrived for fully classifying the family, but he constituted as a sub-family a group which he called the *Chondractiniæ*. The definition of this sub-family was fairly similar to Hertwig's definition of the whole *Sagartidæ* but was narrower, and excluded *Adamsia*, *Metridium* and *Calliactis* as well as *Sagartia*. It constituted, however, a very natural group within the main

¹ Hertwig identified one of the "Challenger" anemones as *Sagartia* sp., but, as more recent work has shown, this identification was incorrect. The form in question evidently belongs to the *Chondractiniæ*, and is probably a *Sagartiomorphe* or something similar.

family, and contained the forms best known to its author. The genera included were *Chondractinia*, *Hormathia*, *Chitonactis*, *Actinauge* and *Paraphellia*.

In 1892 J. A. Simon recognised two sub-groups within the *Sagartidæ*—the *Aiptasinæ*, with the sphincter endodermal or absent, and the *Sagartinæ*, with a strong mesoglœal sphincter. Among the latter he distinguished *Sagartians* without, and *Phellians* with, a cuticle.

In 1893 J. P. McMurrich adopted Haddon's *Chondractinæ*, at the same time suggesting that it might be almost identical with Verrill's *Phellinæ*. However, the anatomy of *Phellia* was not then understood. McMurrich had previously suggested himself a division of the *Sagartidæ* into *Phellinæ* and *Sargartinæ*, but he adopted Haddon's subfamily as being more extensive than, and probably including, the genus *Phellia*. His arrangement therefore is—

Sub-family *SAGARTINÆ*.

“*Sagartidæ* with the ectoderm naked, the acontia being emitted from the mouth and through the column-wall, in which definite openings (cinclides) are present (always ?) for their emission.”

Sub-family *CHONDRACTININÆ*, Haddon.

“*Sagartidæ* with thick column wall, usually with the upper portion (capitulum) different in character from the lower (scapus) and capable of being entirely inverted: the scapus provided with an external cuticle and usually nodulated or warty; the sphincter strong and embedded in the mesoglœa; only the six primary pairs of mesenteries perfect and at the same time nongonophoric; acontia emitted by the mouth only, there being no cinclides.”

This definition of the *Chondractininæ* is not exactly Haddon's original one, but does not differ from it in anything important.

Also in 1893 O. Carlgren (12, pp. 86–7) discussed the inatter. He showed that in some *Sagartias* the primary mesenteries were *fertile*, thus still further removing them from Hertwig's *Sagartidæ*. He kept to the *Sagartinæ* and *Phellinæ*, but added a new sub-family, the *Metridinæ*. His *Phellinæ* was practically identical with Haddon's *Chondractinæ*.

tiniae, but he included *Phellia* in it and went back to the old name; *Phellia* was still not understood as regards its anatomy, although Verrill had said a little about it in 1867.

It will be noted that by this time the "Sagartidae" exhibited only one differential character common to all of them—the presence of acontia. *Aiptasia* had proved an exception to the mesogloal sphincter rule, the number of perfect mesenteries and distribution of gonads were shown to be variable, and cinclides were proved to be present in some cases and absent in others. Cuticle also was present or not in different cases. Even a pedal disc was not invariably present (e. g. *Ilyactis*).

In 1897 C. R. Kwietniewski (55) discussed the family at length, and noticed that the acontia present practically the only feature common to all members of it. He ends up with a division of the family similar to Simon's.

In 1898 A. C. Haddon (44, pp. 446-7) briefly reviewed the family history and adopted a new arrangement of sub-families—an arrangement also suggested in 1898 by O. Carlgren. By this time more was known of the anatomy of *Phellia*, and it was realised that it was quite different from the Chondractiniæ, and must be placed in a sub-family apart, which sub-family, of course, was Verrill's original *Phellinæ*, containing *Phellia* only. I repeat Haddon's definitions here in full, since they represent the most recent classification of the family before 1918, and are important for reference.

Family SAGARTIIDÆ, Gosse.

"Actiniinæ with a contractile pedal disc; body-wall smooth, or provided with verrucæ or tubercles, and usually perforated by cinclides, with or without a cuticle. Tentacles usually numerous and retractile, not very long, smooth, simple and generally entacmeous. Sphincter muscle characteristically well developed and mesogloal, occasionally diffuse endodermal, or even absent. At least six pairs of perfect mesenteries; the first cycle of six pairs of mesenteries may be fertile or sterile. Acontia present."

Sub-family AIPTASIINÆ, Simon.

"Sagartiidae in which the sphincter muscle is either absent or very feebly developed and mesogloal, or diffuse and endodermal."

Sub-family *SAGARTIINÆ*, Verrill.

“Sagartiidae with more than six pairs of perfect mesenteries, of which the six pairs of primary mesenteries are fertile, except the directives in some species; body-wall soft; no tubercles, but verrucae (suckers) may be present in the upper part of the column; cinclides present (chiefly ectodermal invaginations); one or two gonidial grooves; strong mesogloal sphincter muscle.”

Sub-family *PHELLIINÆ*, Verrill.

“Sagartiidae with usually an elongated column, the capitular portion of which is generally delicate and extensile; body-wall provided with a cuticle, but without any solid or hollow processes, such as tubercles, vesicles, or suckers; no cinclides. Tentacles simple, neither very numerous nor very long. Only six pairs of perfect mesenteries which alone are fertile. The remaining mesenteries are usually feebly developed. The retractor muscles are very strongly developed on the primary mesenteries. Acontia usually feebly developed, and emitted only through the mouth. Strong mesogloal sphincter muscle.”

Sub-family *METRIDIINÆ*, Carlgren.

“Sagartiidae with six or more pairs of perfect mesenteries, of which the six pairs of primary mesenteries are sterile; usually one gonidial groove with its pair of directives, but more may occur; body-wall relatively thin, and without a cuticle; cinclides present (chiefly endodermal evaginations); well-developed mesogloal sphincter muscle.”

Sub-family *CHONDRACTINIINÆ*, Haddon.

“Sagartiidae with only six pairs of perfect mesenteries, which alone of the well-developed mesenteries are sterile; two gonidial grooves and two pairs of directives; body-wall usually thick, with a cuticle and often nodulated; cinclides absent (?); acontia rarely emitted, and then by the mouth only; strong mesogloal sphincter muscle.”

Of these sub-families, the *Sagartiinæ* corresponds to the *Sagartinae* used by Carlgren in 1893; the *Metridiinæ* to Carlgren's sub-family with *Aiptasia* removed; and the *Chondractiniinae* to Carlgren's *Phelliinæ* with *Phellia* removed from it.

In work published more recently (1898, 1904), J. P. McMurrich did not accept Haddon's arrangement for various reasons, and returned to Carlgren's three sub-families.

In 1918 G. C. Bourne (10) published descriptions of a

number of Phellids, and discussed very fully the relationships of the Phelliinæ (as understood by Haddon) to the other Actiniaria. He limited the Phelliinæ to Phellia, Decaphellia, and possibly Halcampactis, agreeing with Haddon in separating these forms from the Chondractiniinæ. He analysed the characteristics of the Phelliinæ, discussed the occurrence of certain of their characters, considered singly, among other Actiniina, and showed quite conclusively that, going by *the sum of the more important characters* rather than by one or two somewhat arbitrarily selected, they incline on the balance rather to the Halcampidæ than to any of the sub-families of the Sagartiidæ. He showed that acontia, the mesogloæal sphincter and certain other characters vary independently within the Actiniina. He adopted a hypothesis which would account for the appearance or disappearance of acontia in groups having very different combinations of other characters, and claimed that this would get rid, once for all, of the idea that the presence of acontia is such a positive mark of inter-relation that all forms possessing it must be united in a single family. The main conclusions reached were that the Sagartiidæ must be broken up, that the Phelliinæ must form a distinct family approximating to the Halcampidæ, and that the sum-of-the-characters principle must be generally applied in classifying the Actiniina.

PARACTIDÆ.

R. Hertwig founded a family which he called Paractidæ in 1882 (51, p. 41), and which he defined as "Hexactiniæ, with numerous perfect septa, and with very contractile, moderately long tentacles, which can be completely covered; circular muscle very strong, mesodermal." He placed in this family, as his first genus, Paractis, M. Edw., and also included Dysactis, Tealidium, Antholoba and Ophiodiscus.

In 1883 A. Andres (2, p. 471), set up, independently of Hertwig, a sub-family Paractidæ of his family Actiniinæ. He defined it thus:

“*Forma*.—Base più o meno aderente. Colonna variiforme, contrattile, liscia, senza pori, tubercoli, verruche o rivestimenti. Margine talora presente ma semplice e non sviluppato; non mai crenulato e fornito di acroragi. Tentacoli policicli, conici; retrattili; Colore, Dimensione e Giacitura vari.” This family contained the genera *Paranthus*, *Paractinia* and *Paractis*.

Of these two families that of Hertwig has priority. The exact standing of the forms referred by Andres to his own family is not yet known in all cases, but *Paranthus* has been anatomically investigated, and has been referred to Hertwig’s *Paractidæ* on structural grounds. It is hardly probable that Andres’ family will stand, even under a new name, when the anatomy of all its members is known. Its forms can be referred to their correct positions one at a time as more is known of them. It is the family of Hertwig, to which the name *Paractidæ* rightly belongs, that we shall follow here.

In 1893 J. P. McMurrich (60, p. 160) widened the definition so as to include forms with few perfect mesenteries, and he omitted any definition of the tentacles.

In 1893 O. Carlgren (12, p. 64) gave a history and discussion of the family. He re-defined the family as follows: “Actininen mit Fussscheibe, mit sehr contractilen, mässig langen Tentakeln und zahlreichen, vollständigen Septen. Septenpaare der höheren Cyclus (vom dritten oder vierten an) unregelmässig entwickelt, so dass das Septum, das seine Längsmuskeln gegen den im Allgemeinen nächst niederen Septencyclus kehrt, mehr entwickelt ist als das andere in demselben Paare. Radialmuskulatur der Mundscheibe und Längsmuskulatur der Tentakeln im Allgemeinen mesodermal. Sphinkter mesodermal. Acontien und Cinclides fehlen.” But in a note at the end of this paper (12, p. 137), in the light of some new information regarding the genus *Paractis*, he transferred the above definition from the *Paractidæ* to a new family *Actinostolidæ*, containing the genera *Actinostola* and *Stomphia*, and made a fresh diagnosis for the *Paractidæ*.

proper, including Paractis. This diagnosis was "Actininen mit Fuss scheibe, mit mässig langen Tentakeln und gewöhnlich zahlreichen, vollständigen Septen. Septen in demselben Paare regelmässig entwickelt. Radialmuskulatur der Mundscheibe und Längsmuskulatur der Tentakeln im Allgemeinen mesodermal. Sphinkter mesodermal, gewöhnlich wohl entwickelt. Acontien und Cinclides fehlen."

There is little to add. Hertwig's Paractidæ has been generally accepted with modifications, and the Actinostolidæ and Paractidæ as defined by Carlgren in 1893 have become sub-families—Actinostolinæ and Paractinæ—within the main family (see Carlgren, 1899, pp. 26-7). The features possessed in common by the forms which have been included in the family from time to time are the presence of a base and of a mesoglœal sphincter and the absence of acontia and cinclides.

In 1918 O. Carlgren (23) contributed fresh details of the anatomy of *Polysiphonia tuberosa* Hertwig, and claimed that on account of the very unusual way in which its mesenteries develop it should be placed in another sub-family (Polysiphoniinae) from the Paractinæ and Actinostolinæ, or in a family Polysiphoniidæ if it should be considered that the Paractinæ and Actinostolinæ had more than sub-family rank. Details of the Polysiphoniinae will be found on p. 549.

III. DESCRIPTION OF CERTAIN ANATOMICAL DETAILS.

I should like to establish one or two anatomical particulars before going further, because some of the statements which will be made later on are based upon them.

AIPTASIA COUCHII, Cocks.

It has long been impossible to define the genus *Aiptasia* quite exactly, because of the absence of any description of the anatomy of British specimens of the genotype—*A. couchii*. Pax has described, it is true, the anatomy of an *Aiptasia* from Gomera in the Canary Islands, which he

identifies as *A. couchii* (see 70, p. 337); but since it does not agree in all respects with the structure I find to be characteristic of actual British specimens, I conclude that it may be a different species closely allied to *A. couchii*. One might easily expect this to be the case in a locality so far from Britain as Gomera. I have obtained from Plymouth several living specimens of *A. couchii*, one of them large and the others rather small. These agree completely with Gosse's description of the species. A study of sections of some of them reveals the following details. Six pairs of mesenteries alone are perfect, including the two pairs of directives. There is no sharp distinction between the primary mesenteries and those of the other cycles, save as regards the perfection of the former only—i.e. the mesenteries are not distinguished into macrocnemes and microcnemes.¹ The retractor muscles are fairly weak and perfectly diffuse (see Text-fig. 20). My material unfortunately does not show which mesenteries are fertile. Well-developed acontia are present and the mesenterial filaments possess ciliated lobes. Cinclides present. Longitudinal musculature of tentacles and radial musculature of oral disc ectodermal. At the extreme margin of the body is a very weak sphincter muscle, completely embedded in the mesogloea. It is quite poorly developed, and consists, as seen in section, of a thin chain of cavities in which and round the borders of which the muscle-fibres are arranged. My sections of it are very clear, and admit no possibility of doubt as to its existence. A small portion of this sphincter is shown in Pl. 22, fig. 10, which also exhibits the large zooxanthellæ with which the endoderm is crowded. In some sections it is possible to see quite clearly that in the uppermost parts, at all events, of the body-wall and actinopharynx an *ectodermal* longitudinal musculature is present. It is feebly developed, but in some cases the fibres are supported by distinct processes of the mesogloea. I have drawn a small

¹ See p. 456 for an exact definition of the terms "macrocneme" and "microcneme."

portion of a transverse section of one of the actinopharyngeal grooves in Pl. 22, fig. 11, where these short processes seem best developed. Apparently a nerve-layer accompanies this musculature.

The *Aiptasia* from Gomera described by Pax as *A. couchii* differs from the true British species in that it possesses no mesogloœal sphincter. Also, it can have more tentacles—72, whereas our form seems limited to 48. There are certain anemones in which there is apparently a constant maximum number of tentacles. Further, Pax does not mention that his anemone has any ectodermal musculature in body-wall and actinopharynx. These differences are enough to separate it from *A. couchii*, and I propose for it the name *A. paxi*. Its generic name should be *Aiptasiomorpha* (see p. 530), not *Aiptasia*. The effect of the discovery of a mesogloœal sphincter in *A. couchii* on the generic synonymy is discussed on p. 531.

SAGARTIA MINIATA, Gosse.

This is the type-species of the genus *Sagartia*, and a short statement of its essential characteristics will help to make later discussions clearer.

The body-wall is smooth when distended, finely corrugated otherwise, and is provided with more or less conspicuous suckers which are at their best development on the upper part of the body. Cinclides are present, but I will leave the more detailed description of these till the next section (see p. 451). Tentacles typically in five cycles, on the plan $12 + 12 + 24 + 48 + 96 = 192$. This formula is liable to variations affecting one or more sectors of the animal. The lips are strongly corrugated. The species is clearly characterised and separated from its nearest relatives by colour and markings, but that does not especially concern us here and I hope to deal with it in another place. A fairly large and quite typical individual of which I have a series of sections has five cycles of mesenteries. They are developed with perfect regularity save in one sector, in which two tertiary

pairs are absent, their absence carrying with it the further absence of two pairs belonging to the fourth cycle, and four belonging to the fifth. This is simply a small individual irregularity, hardly any specimen of this species developing exactly according to formula. The mesenterial formula for this specimen, then, is 6 p. + 6 p. + 10 p. + 22 p. + 44 p. = 88 p. Of these, two pairs are directives and are related to the two actinopharyngeal grooves. Twenty-two pairs are perfect—cycles 1-3 inclusive. Only the perfect mesenteries have definite retractor muscles, and these are strong and diffuse, with slender well-branched processes (see Text-figs. 13-16). There is no sharp distinction of the mesenteries into macrocnemes and microcnemes,¹ the cycles being graded. Every perfect mesentery bears two mesenterial stomata—a small labial and a larger parietal. The zone containing the labial stomata is about 1.7 mm. deep, and that containing the others about 2.6 mm. Filaments occur on mesenteries of cycles 1-4 (inclusive); they are well developed. Ciliated lobes are present. The mesenteries of the fifth cycle are very small, and are better developed in the highest and lowest regions of the body than elsewhere. Sections and dissections of other specimens show that gonads develop on mesenteries of cycles 1-3 inclusive, at least, even the directives being fertile in some cases at any rate. Acontia are present in abundance. Definite basilar muscles are developed. The longitudinal musculature of the tentacles and radial musculature of the oral disc (see Pl. 22, fig. 9) are ectodermal. There is a strong and definite mesogloea sphincter, and I have drawn a typical section of it in Pl. 22, fig. 3.

HALCAMP*A* CHRYSANTHELLUM, Gosse.

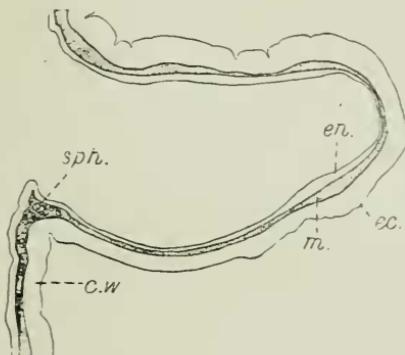
I have discussed the synonymy of the genus *Halcampa* in a former paper (79, pp. 8-10) in correlation with the possession of a mesogloea sphincter by the genotype, *H. chrysanthellum*. I am now able to give a figure showing

¹ See p. 456 for definition of terms "macrocneme" and "microcneme."

a small portion of a section of this sphincter in detail (Pl. 22, fig. 7). Its general situation in the body-margin is better understood from Text-fig. 1.

The specimen illustrated is from Plymouth. The sphincter in this species is small and perhaps weak, but distinct.

TEXT-FIG. 1.



Longitudinal section of a tentacle and of the body-margin of *Halcampa chrysanthellum* to show position of sphincter.
c.w. Column wall. *ec.* Ectoderm. *en.* Endoderm. *m.* Mesogloea.
sph. Sphincter.

FLOSMARIS PHELLIOIDES, n. gen., n. sp.

The single specimen of this species which I have been able to examine was kindly lent me by Prof. J. Stanley Gardiner. It is labelled "Hulule: sand—close to low tide."

There is a quite distinct pedal disc, which is smooth and very thin-walled and flabby, showing the mesenterial insertions through its wall. The column is divided distinctly into scapus and capitulum; it is longer than wide, and the scapus is of much greater extent than the capitulum. Wall of scapus fairly thin throughout, not stiff enough to support itself; in the lower part excessively thin, flabby, and semi-transparent. This thinnest lower part is smooth and devoid of sand-grains; but the main part of the scapus is more opaque, though not entirely so, and is covered with many small papillæ or suckers to which white grains of sand are

firmly attached. The capitulum is fairly smooth and devoid of sand-grains. Margin tentaculate. I could see no trace of cuticle even on the scapus. Whether cinclides are present or not is uncertain, but careful examination of the wall failed to reveal any, and I think they are probably absent.

Internally there are twenty-four pairs of mesenteries visible to dissection. These are sharply divided into macrocnemes¹ and microcnemes. The first two cycles (6p. + 6p.) are macrocnemes; every one of them possesses a circumscribed retractor plainly visible to the unaided eye, a large gonad, and a well-developed filament; all of them are perfect. There are two pairs of directives. The microcnemes form simply twelve pairs of narrow streaks on the body-wall, and in the portion of the animal dissected they bore no trace of gonad, filament, or retractor, so that if any of these were present they would be so small as to be invisible to the naked eye or to a lens. These microcnemes are of course not perfect. Well-marked but not greatly developed acontia are present on some at least of the macrocnemes. In the case of the macrocnemes there is a tendency for the gonad and filament to be more extensive, or to end at a lower level in the coelenteron, on one partner than on the other, of each pair; the latter point affects the retractors too. In the case of the primary macrocnemes, the eight *Edwardsia*-mesenteries have the endings of these structures rather lower than the other four primaries; and the four lateral mesenteries of these eight have them ending lowest of all. The lowest ends of those of the secondary macrocnemes are generally speaking rather higher up than those of the primary ones, and here, if those of one partner end lower than those of the other, it is the ventral and not the dorsal partner in each pair which is affected—the opposite of what takes place in the case of the primaries. I should add that the above statements are made from a very careful dissection of one-half of the lower three-fourths of the animal (the uppermost end being devoted to sections), aided by a less detailed study of the other half

¹ See definition on p. 456.

—I did not wish to break the specimen up too much. But the animal is large and well preserved, and what I did see of the second half without injuring it unduly allowed me to see that in most respects it is certainly, and in the rest probably, exactly identical in essentials with the first. It will be noted that although there are two cycles of macrocnemes here, the transition from cycle 2 to the microcnemes is very abrupt, there being no intervening cycle or cycles of moderately developed mesenteries between the fully-developed macrocnemes of cycle 2 and the rudimentary microcnemes of cycle 3.

Sections of the upper part of the body confirm many of the above details and provide others. The retractors of the macrocnemes vary in size in individual mesenteries, but as a whole there is not much difference between the primary and secondary macrocnemes in this respect. The macrocnemes and microcnemes bear well-developed parietal muscles. In the uppermost part of the body some additional microcnemes, over and above the twelve pairs visible on dissection, are present. Some of the microcnemes bear acontia at a fairly high level. The longitudinal muscle of the tentacles and radial muscle of the disc are fairly developed and ectodermal. A mesogloal sphincter is present, but it is rather small and appears to be entirely confined to the upper part of the capitulum, just below the margin. I cannot as yet be sure about cuticle, but although there is evidently no conspicuous development of it, a certain amount may perhaps be present on the scapus. I hope to add to this description sooner or later.

IV. DISCUSSION OF ACONTIA AND CINCLIDES.

(In relation to the scheme of classification which follows.)

Acontia.

It will be evident from the foregoing brief account of the history of the family Sagartiidae that the majority of authors consider the chief diagnostic character of the family to be the

possession by its members of acontia. Under the heading "Sagartiidae" has been gathered together a miscellaneous collection of forms differing very considerably among themselves, but possessing no other common feature save the acontia. There is, it is true, a second character found in the majority of them—a mesogloal sphincter—but this is not universal and occurs in many forms devoid of acontia.

One might say that all anemones are related to one another because all have mesenterial filaments. Although this is the case, it in no way follows that all anemones must be included in one family, or considered as being very *closely* related, on account of that single feature, however much they may differ among themselves in other ways. Now an acontium can only be regarded as a specialised form of mesenterial filament. It is distinguishable from the latter by certain histological details and by the fact that it is free from the edge of the mesentery save at one end. There is therefore no reason why two given forms should be placed in the same family or even considered to be very closely related because both possess acontia if they are very different in other ways. It is quite a possibility, as Bourne has pointed out (10, p. 81), that acontia (which are not all identical in structure) may have been independently acquired by several groups of Actinians. I am personally of the opinion that it is more probable that all forms possessing them are descended from a common ancestor, as I shall repeat with what evidence there is in favour of my view later on. But even if this is the case, we do not know how old the group is, and it may be quite old enough to allow for a good deal of divergent evolution since the acquisition of acontia. There is no reason to suppose that that acquisition may not have been at a fairly early stage, since an acontium is but a variety of filament, and filaments are present even in the earliest known anemones. This does not, however, dispense with the acontium character as a useful one in classification, provided it is used as one among others and is not made more important than anything else.

A transverse section of a typical acontium is shown in Pl. 22, fig. 4. The figure displays the general kidney-shaped form typical of acontia in section, the axis of mesogloea, the large thick-walled nematocysts arranged fanwise on one side of the acontium, and the presence of granular gland-cells. This particular acontium is one belonging to *Sagartia miniata*, and is stained with borax carmine and picro-indigo-carmine, which picks out the sting-cells very clearly.

Acontia, in general, are slender white or coloured threads attached to the borders of mesenteries at one end and quite free at the other. Their surface is ciliated, and if a piece of acontium is detached from the animal and placed on a slide in a little sea-water, it may exhibit fairly active serpentine movements on its own account for some time. An acontium is mainly characterised histologically by the possession of numerous and often extremely large thick-walled nematocysts. It has also a delicate layer of longitudinally disposed muscle-fibres, which do not always bear the same relation to the axis of mesogloea. Many gland-cells may be present. A simple mesenterial filament resembles an acontium in general form and in the possession of gland-cells and nematocysts, but it lacks muscle-fibres and its nematocysts are typically smaller and less numerous.

Acontia are emitted more or less copiously through the mouth (according to the kind of anemone possessing them) under certain circumstances, such as irritation. The freedom with which they are put forth varies in different species. They doubtless help to paralyse prey and to defend the animal. If there is a wound they come out through it, and if pores are present in the body-wall these also may be used as means of egress. The cilia covering the acontia may help in their extrusion, but the chief facts about their emission will be dealt with in considering the cinclides. Acontia are more abundantly and better developed in some genera than in others, and in some cases may be partially reduced or even quite rudimentary, so that great care is needed to detect them.

Cinclides.

The definite pores which occur in the body-walls of certain anemones, and to which Gosse gave the name *cinclides*, seem to have been first noticed by Rapp in *Calliactis parasitica* ("*Sagartia*" *parasitica*). Various authors have confirmed the fact of their existence. Gosse considered that the purpose of the cinclides was to let out acontia, and a connection between the two often seems to be assumed. It is an idea which has gradually gained weight in my mind, that the relationship between acontia and cinclides is really secondary and in a sense accidental, and that the acontia emerge through the cinclides *because the cinclides happen to be there*. If this is the case, what is the primary function of the cinclides? It seems likely that they are structures typical of more or less delicate-bodied¹ anemones which provide for the establishment of a relationship between the water in the animal's coelenteron and the sea outside; and that they provide a line of least resistance for the escape of some of this water on sudden violent contraction of the animal, thus preventing a definite rupture of the wall. There is a good deal of evidence in support of this view, which I will set forth.

In the first place, a number of anemones possess cinclides but have no acontia. The pores found in these species have not before been actually termed "cinclides" as a rule, but in structure and relationships they are identical with some *Sagartian* cinclides, and I shall henceforward apply the name to them. I had the opportunity of observing, through the kindness of Mr. H. C. Chadwick, of the Port Erin Biological Station, the habits of two living specimens of *Peachia hastata* in good health. This species has no acontia, but its physa is perforated by very many cinclides arranged in longitudinal rows. It is not easy to observe these cinclides

¹ The wall of the body in the genus *Calliactis* may be fairly thick and firm, and is therefore less delicate than in many cinclis-bearing forms. It is perhaps a case in which strength of body-wall will eventually be gained at the expense of loss of the cinclides.

in a living animal under water, because it does not keep still, and is ever changing its shape. However, I succeeded in getting a clear view of them, even with a one-sixth objective. They have the appearance of little windows or thin diaphragms in the body-wall, which are pale by transmitted light; and in the centre of the window is a small aperture the size of which varies from time to time.¹ The animal, therefore, keeps these pores open, sometimes at any rate, when at rest and in a healthy condition, and it seems evident that they have some connection with water-currents. In longitudinal sections of the cinclis-region of one of these specimens one can see that the pores may have a structure similar to some of the cinclides in *Sagartia*. In some cases it seems that they originated by an ingrowth of the ectoderm, which pushed its way through into the interior. One such *ectodermal invagination* is figured in Pl. 22, fig. 6. It will be seen that the mesogloea and muscular layer are interrupted by the penetrating ectoderm, which is itself penetrated by a definite channel. The resemblance of this cinclis to the one drawn in Pl. 22, fig. 2, from near the edge of the base of *Sagartia miniata* is most striking.

Other anemones possessing cinclides but no acontia are the following: Hertwig describes pores in the physa of *Halcampoides clavus* which, from both his description and figures, are evidently ectodermal invaginations comparable to some of those near the base in *Sagartia miniata*. Prof. G. C. Bourne tells me that he has found pores in the physa of an *Edwardsia*, whose relations are just those of cinclides. *Harenactis attenuata* has a definite longitudinal row of cinclides communicating with each exocoel and each endocoel in the upper part of the long vermiform body. Other instances might be mentioned.

Let us now turn to those forms in which both acontia and cinclides occur. Gosse discusses cinclides in his 'Actinologia Britannica,' pp. xxv–xxix. He records observations of *open*

¹ I am not sure that the "window" is invariably perforated, but it is at least frequently so.

cinclides in specimens which were presumably *at rest*; and that a very thin membrane may often be detected across the mouth of an open cinclis. He attributes this membrane to the constant sloughing of mucus which takes place in anemones. He records also that in an animal which had emitted acontia there were open cinclides through which no acontia protruded as well. He attributes the emission of the acontia to the currents of water which are forced out of the animal when it contracts, and notes in connection with this that acontia frequently come out of cinclides as *loops*—not free end first—and that more than one acontium may protrude through one cinclis. G. Y. Dixon (27) subscribes to Gosse's account of the cinclides from his own observations, except as regards the thin film across the mouth of an open cinclis. Dixon states that in fully expanded animals (he is dealing with *Sagartia venusta*, *S. nivea*, and *S. miniata*) when at rest the cinclides are generally open, and suggests that the emission of acontia is not their only function, but that, as Agassiz has supposed, they take part in providing communication between the interior of the animal and the surrounding water. Milne-Edwards attributes the liberation of water as well as acontia to the cinclides, and Hertwig suggests the passing in and out of water as the function of the pores of *Halcampoides clavus*.

I have not experimented at all exhaustively with anemones with regard to cinclides, but what observations I have made are enough to show that the connection between acontia and cinclides is secondary and accidental. If one suddenly squirts a little water containing carmine powder (I did it with *S. miniata* and *C. pedunculatus*) into an anemone's mouth with a fountain-pen filler, when the anemone is expanded and pretty well distended with water, this causes the body to contract suddenly and violently, and one can then see very clearly that little jets of carmine are projected with great force through the cinclides, and travel to a considerable distance from the animal before being lost in the water. They come out *instantaneously*, the cinclides acting as safety-

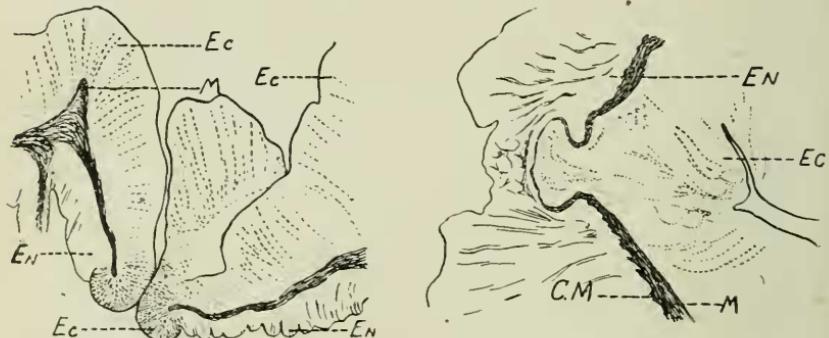
valves against rupture of the wall at the first contraction-jerk, the main volume of the carmine returning more slowly through the mouth. These jets of water and carmine are *not* generally followed by the protrusion of acontia quite immediately, the latter seeming on the whole to be forced out only after a good deal of contraction. And of course in any case the mouth is their chief exit. Apart from this I have seen, under the microscope, water spurting from the cinclides of a contracting animal. On one occasion I had a *Sagartia miniata* under the microscope, and on gently pressing it I saw a jet of water come out of a cinclis, followed by an acontium. I have also seen the acontia forced out by the water as loops, forced into the tentacles by water currents, and forced through the base of an animal just removed from a stone. In the last case the water would be expelled from the contracting animal through small invisible wounds or very thin places such as do occur in the pedal disc, and acontia would accompany the water.

All this seems to show that the acontia come out anywhere where the least resistance is offered, that the cinclides act as safety-valves for water, and that the acontia come out of them incidentally, being propelled in all directions by the escaping water. What, if any, other functions the cinclides have I do not know, and a good deal of investigation, not necessary for my present purpose, would be needed to find out.

In *Sagartia miniata* and *Cerens pedunculatus* they sometimes seem to close when one would expect them to be open. In those cases in which I have most clearly observed open cinclides in one of these species when completely *at rest*, there was certainly a film such as Gosse described stretching across the open mouth of the cinclis. This film may be the *diaphragm*, which will presently be described as characteristic of certain cinclides, and which, as is shown by sections, may or may not be penetrated by a definite channel or aperture. It would be quite natural for the aperture, if present, to be kept closed by its sphincter in a state of rest—some of the

time at any rate. When a cinclides emitted water, either the hole in the diaphragm would be opened (this I have seen taking place), or else the water would rupture the diaphragm in its excessively thin central part, which, as will be seen, is specially constructed so as to heal again easily. In *Peachia* the cinclides were in many cases, when I saw them, quite definitely open—the aperture in the centre of each “window” being quite clear and free from a covering film. In this species the life-conditions are not those of *Sagartia*, and it may well be that the cinclides have a more extended function

TEXT-FIGS. 2 AND 3.



Sections of cinclides of *Sagartia miniata*. Fig. 2 on left, 3 on right. See p. 452. *C.M.* Endodermal circular musculature. *Ec.* Ectoderm. *En.* Endoderm. *M.* Mesogloea.

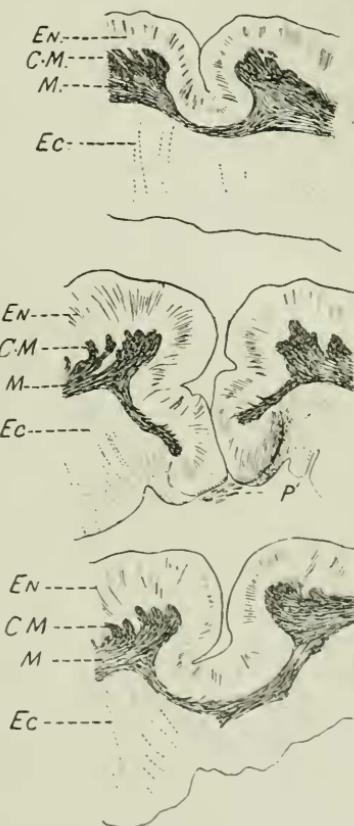
connected with the frequent change in form of the body as well as that of acting as safety-valves.

It seems, therefore, a fair conclusion from the above-mentioned data that cinclides and acontia are characters which may have been independently acquired, and have become more or less secondarily connected in some cases. It does not seem unlikely that the cinclides came first, as those species which possess them but do not possess acontia are fairly primitive forms. This being so, although there is no reason why “presence of acontia” and “presence of cinclides” should not be used as two among other characters in classifica-

tion, we are not necessarily to suppose, when the two are found in conjunction, that this forms a high double specialisation, all forms possessing which must be united in a single family. It should also be borne in mind that many forms possessing acontia are devoid of cinclides, and this makes it an additional advantage to treat the two characters separately.

Before leaving the question of cinclides, I think it will be of value to describe their mode of occurrence in a single typical case. *Sagarta miniata* affords a convenient example. In a specimen of the species of which I have a complete series of sections the following details are found. The uppermost margin of the body is occupied by the sphincter muscle, so that a zone of about 2.3 mm. below the margin is quite free from cinclides, which would interfere with the sphincter if they penetrated it. Below this is a zone about 2.8 mm. deep in which occur many cinclides. This is followed by a wider belt about 3.4 mm. in extent, which is devoid of cinclides. Lastly, the zone of the body-wall immediately above the base, a zone about 1.3 mm. deep, is again occupied by cinclides. That is to say, there are two

TEXT-FIGS. 4-6.



Sections of cinclides of *Sagarta miniata*. Fig. 4 above, 5 in centre, 6 below. Lettering as on Text-fig. 2, p. 450. Also P^1 . Disintegrating epithelial mass.

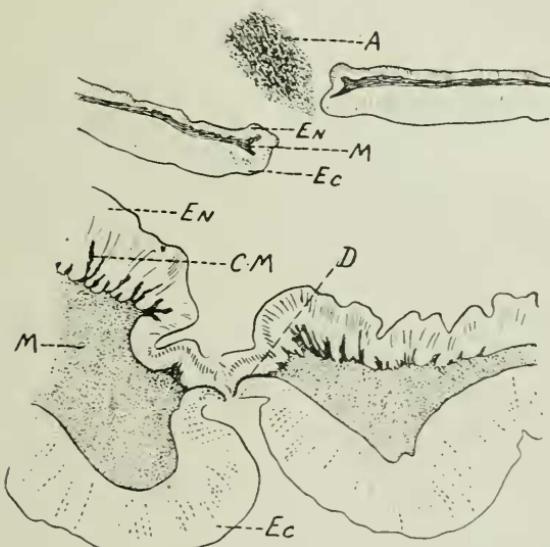
zones in which cinclides occur, separated by a barren zone. The lower zone is as near the edge of the pedal disc as possible, and the upper zone is as near to the uppermost part of the body as it can be without interfering with the sphincter. This distribution is significant in connection with the function of the cinclides as safety-valves, etc., because it means that they occur near the corners of the exocœls and endocœls which are furthest from the mouth or main exit. Furthermore, the zone in which the upper cinclides occur coincides exactly with that occupied by the labial and parietal stomata of the mesenteries, so that the pores allowing water to pass through the mesenteries are on a level with those allowing it to escape through a wall.

It is evident that the cinclides of the lower zone are not typically identical in structure with those of the upper. One may say that frequently the upper-zone cinclides are chiefly or wholly outpushings or *evaginations* of the *endoderm*, whereas those of the lower zone are often *invaginations* of the *ectoderm*. Moreover, a more complex structure may be detected in many of the upper cinclides than I have seen in any of the lower ones examined. Text fig. 2¹ and Pl. 22, fig. 2, show two good examples of lower-zone cinclides. Both show an interruption in the rather thin mesoglœa (*M.*), and a channel penetrating the ectoderm (*E.*, *Ec.*), which has pushed its way right through the wall and forms two little lips on the inner side. Text-fig. 3 shows another, in which the ectoderm is just in the act of penetrating the mesoglœa, but has not actually gone through the endoderm yet. Text-fig. 4, on the other hand, shows one of the upper ciulclides in a young condition, in which it is growing out *through* the mesoglœa *from* the endoderm. Text-fig. 6 is a section cut a little to one side of the centre of the same cinclis as that shown in Text-fig. 5, and it demonstrates the outpushing from the endoderm very

¹ In all the text-figures of cinclides (2-9) I have indicated the general directions of the endoderm-cells by continuous strokes, those of the ectoderm cells by interrupted lines. The mesoglœa is dotted or shaded more darkly.

well. Text-fig. 9 shows another similar case, the section here also being cut a little to one side of the central perforation. Text-figs. 5, 8, and Pl. 22, fig. 1, show sections passing exactly through the centre of three of these upper cinclides. In these cases it will be seen that the main mesogloea and the endodermal circular muscle cease abruptly on either side of the

TEXT-FIGS. 7 AND 8.



Sections of cinclides of *Sagartia miniata*. Fig. 7 above.
8 below. Lettering as on Text-fig. 2, p. 450. Also A. Acontium.
D. Diaphragm.

cinclis, but that stretching across the interrupted part there is a little very delicate diaphragm (D.), consisting of practically nothing but muscle-fibres. The diaphragm itself is interrupted in its middle, putting the ectoderm and endoderm in communication with one another. But although there is also sometimes a definite channel penetrating the epithelium as well as the diaphragm (Text-fig. 5), this often seems to be absent or at any rate irregular (Text-fig. 8, and Pl. 22,

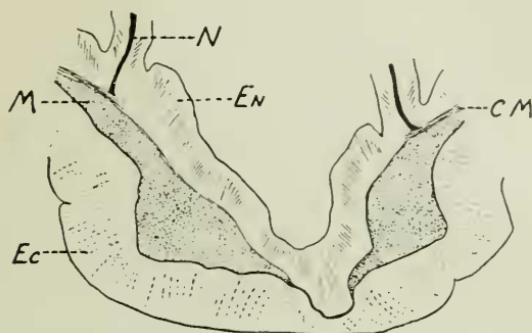
fig. 1¹). (In preserved specimens, of course, the body-wall is often in a somewhat contracted condition, and the cinclides seen in sections are generally closed ones, the two opposing walls of the channel, when it is present, being pressed against each other.) In some cases one can see that in *both longitudinal and transverse* sections the muscle-fibres composing the little diaphragm are cut *crosswise*. This implies that they run circularly round the diaphragm and form a little sphincter-muscle, which in life is no doubt capable of keeping the orifice of the diaphragm closed. In Pl. 22, fig. 5, is seen the diaphragm of a cinclis, much enlarged, as seen with a $\frac{1}{2}$ oil-immersion objective; it shows the muscle-fibres (which must be derived from the endodermal circular muscle) cut *crosswise* in a *transverse* section of the whole body. Longitudinal sections, if clear, present a similar appearance. Text-fig. 7 shows an open cinclis with an acontium partly protruding through it.

The fact that some of the cinclides show a definite interruption in the thin muscular diaphragm, but not an actual passage through the epithelium, seems to give additional confirmation to the idea that they act as safety-valves. It is possible that the cinclides of this type, when first formed, are not exactly pores, but are organised "thin places," or "soft spots," or "lines of least resistance," through which water will burst if through any part on sudden violent contraction of the body. It is noticeable that the parts which in these cases present a

¹ It may be noticed that in this figure (Pl. 22, fig. 1) there is a little bridge of endoderm crossing the internal cavity of the cinclis. This is due to the fact that some cinclides have little lips of endoderm on their inner sides, and in this particular section the overhanging edge of one of these lips has got cut across. In this figure, as in Text-fig. 8, it will also be seen that the two cinclides from which these figures were drawn are only partly evaginations of the endoderm, and appear to be partly also ectodermal invagination. They are really more evaginations than they appear to be at first sight, because externally directed papillæ of mesoglea happen to flank the opening of the cinclis and give rather a false impression when more of the parts surrounding the cinclis cannot be seen.

definite interruption (the muscle and the mesogloea) are those which would be least easily renewed after a rupture, whereas the easily-renewed epithelium presents no definite channel. It is not impossible, again, that a cinclis of this kind, once burst open, may retain the channel formed in the epithelium by rupture and regularise it.

TEXT-FIG. 9.



Section of cinclis of *Sagartia miniata*. Lettering as on Text-fig. 2, p. 450. Also N. Mesentery.

There is one point which will be affected by the notes given above. Carlgren included, tentatively and with a query, in his diagnosis of the sub-families Metridiinae and Sagartiinae the character that in the former the cinclides are chiefly endodermal evaginations, and in the latter chiefly ectodermal invaginations. But since it is now seen that both kinds may occur in one animal, not to speak of one species or one genus, that character evidently cannot be used as a family one. The cinclides described by Carlgren for *S. vidnata* are more like those characteristic of the lower zone in *S. miniata* than the others, but are not identical, though they are ectodermal invaginations. The cinclis figured by Hertwig for *Calliactis parasitica* (*Sagartia parasitica*) looks most like an outpushing of endoderm.

V. DISCUSSION OF CHARACTERS TO BE USED IN CLASSIFICATION.

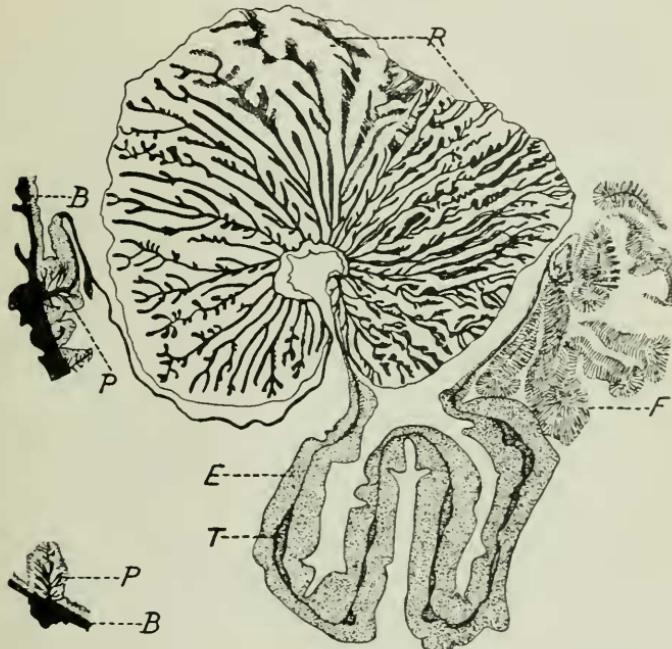
In choosing a series of characters for use in the discussions which follow I have selected those which appear to be the most important and those most generally distributed among the forms with which this paper deals—forms with mesogloal sphincters. I have eliminated characters of merely generic importance and liable to occur anywhere. It is of course impossible to draw a hard-and-fast line between characters which are and are not of sufficient importance to rank as family characters, but I have made my list as fairly as I can.

I have been considerably impressed during the course of my work with the importance of one of the characters affecting the mesenteries. In many forms there is a marked differentiation of the mesenteries into two main types. I am applying to these types throughout the course of this paper the terms *macrocneme* and *microcneme*. I regret that it is necessary to introduce new terms, but I do not feel that it would be wise to risk confusion by not doing so. There are two words already in use—*macromesentery* and *micromesentery*—which would serve my purpose if taken in a certain sense, but I have noticed that different authors mean different things when they use these words, and have therefore introduced new ones to make my meaning clear. By a *macrocneme* I mean a large, perfect mesentery bearing a well-developed retractor muscle (usually "circumscribed" and consequently reniform in section), a gonad, and a well-marked filament; these in addition to a parietal muscle as a rule—generally the latter is very definite. A *microcneme* varies in the exact details of its development in different cases, but is typically reduced to little more than a narrow lamella bearing parietal musculature; as a rule it is not perfect, bears no gonad, no retractor muscle and no well-developed filament. The contrast between a typical *macrocneme* and a typical *microcneme* is well brought out by Text-figs. 11 (*macrocneme* of *Phellia*

phassonesiotes) and 10 (microcneme of *P. phassonesiotes*), which are both drawn to the same scale.

It will be evident that if an anemone possesses a number—say six pairs—of macrocnemes, and all its other mesenteries are microcnemes, the distinction between the two is

TEXT-FIGS. 10 AND 11.



Text-fig. 10 (Below).—Microcneme of *Phellia phassonesiotes*.

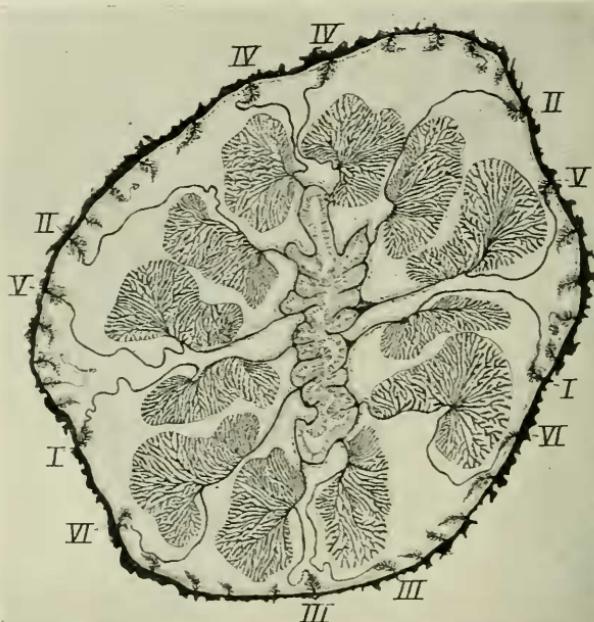
Text-fig. 11 (Above).—Macrocneme of *Phellia phassonesiotes*. Both drawn to same scale. *B.* Body-wall. *E.* Endoderm. *F.* Mesenterial filament. *P.* Parietal muscle. *R.* Retractor. *T.* Testis.

one of the most striking and important features of that form. Text-fig. 12 shows a good example of this. It is a transverse section of *Phellia phassonesiotes*, and shows how the macrocnemes fill up almost the whole coelenteron, whilst the microcnemes are insignificant.

One must add the qualification that in *Diadumene*

schilleriana (Pl. 22, fig. 12) (see p. 521) some of the microcnemes of some *individuals* may develop unusually and produce gonads and retractors. This means that in such individuals the distinction of the mesenteries into macro- and microcnemes is partially lost (see p. 499). Apparently

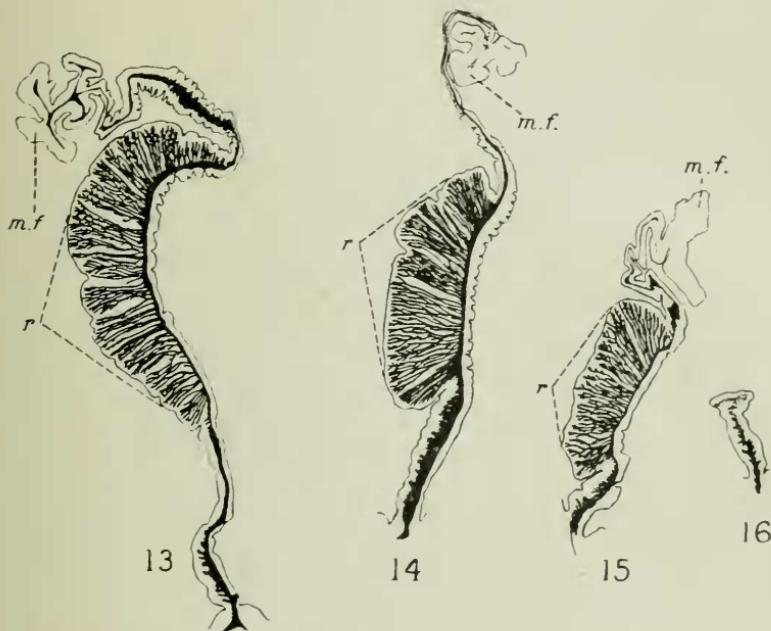
TEXT-FIG. 12.

Transverse section of body of *Phellia phassonesiotes*.

it is not fully marked in this species in any case, although often the macrocnemes alone are fertile and always are alone perfect. The existence of this form, which is intermediate between those in which the division into macro- and microcnemes is fully marked and those in which no such distinction exists, does not alter the main fact of the usefulness of the presence or absence of this distinction as a classificatory character. There are many useful characters between which

intermediates exist. Speaking generally, however, microcnemes are very small and at most bear a small filament and an aconitum, together with an insignificant vestige of longitudinal muscle, or they may be rather broad lamellæ, but devoid of filament, etc. As an exceptional thing a few micro-

TEXT-FIGS. 13-16.



Mesenteries of *Sagartia miniata*, one mesentery from each cycle, of cycles 1-4. All drawn to same scale. *m.f.* Mesenterial filament. *r.* Retractor.

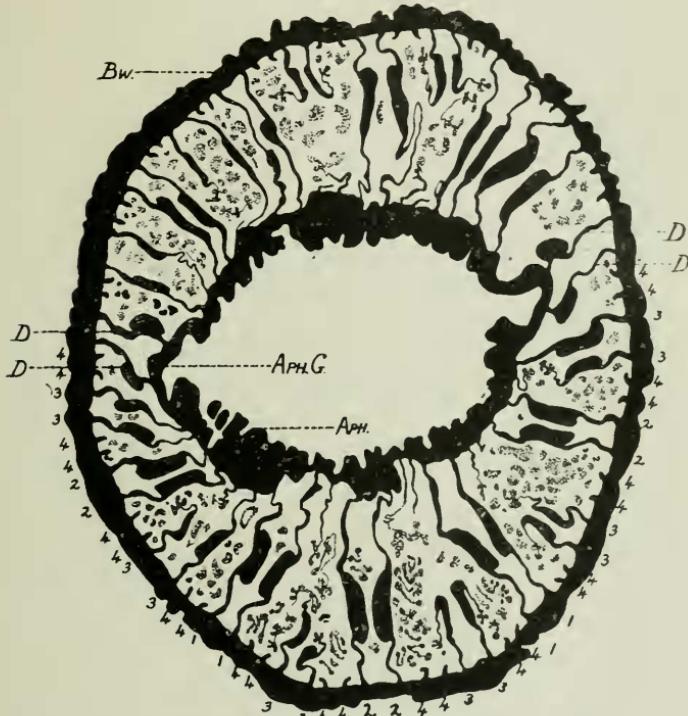
cnemes in *Pelocœtes* (Pl. 22, fig. 13) may develop gonads, filaments, or retractors, but here the distinction into macro- and microcnemes is very definite (see Text-fig. 28), and as a rule the latter are rudimentary. The number of the macrocnemes is in most cases a stable and reliable character. It so happens that most of the forms here dealt with have six pairs of macrocnemes only, but one of them has twelve pairs, and in

other families not under immediate consideration there are other numbers.

In species the mesenteries of which are not differentiated into macro- and microcnemes, it is found that the mesenteries of the first cycle may only differ from those of the second cycle by being a little larger, the second-cycle mesenteries differ from those of the third cycle in the same way, and so on—that is to say, there is a more or less graded series from the oldest cycle downwards and the primaries are not the only mesenteries that are really well developed. The mesenteries of *all* the older cycles bear well-developed retractors and filaments, the sizes of these diminishing as we pass from older cycles to younger ones. Text-fig. 19 shows several mesenteries from one of these forms (*Actinauge richardi*). It includes one primary, one secondary and one tertiary pair of mesenteries, all provided with filament and retractor and exhibiting a graduation in size. The fourth cycle here is still quite small. Text-figs. 13–16 show four mesenteries, one from each of the first four cycles, of *Sagartia miniata*, and bring out the gradation very well. All four figures are drawn to same scale. Among forms of this nature the retractors are typically diffuse, only rarely circumscribed. Two types of diffuse retractor are illustrated in Text-figs. 20 and 21, one of them more perfectly diffuse than the other. In this class of anemones the number of mesenteries which reach and join the actinopharynx—i. e. are perfect—may be six pairs only or may be many pairs. Here again there is not an absolutely clear-cut distinction, because a few species in which the standard number of perfect pairs is six show a tendency to develop seven or eight or even a few more perfect pairs (i. e. one or two more than the six primaries); and in a few species belonging to genera with a higher standard number of perfect mesenteries than six pairs the total number may not be *many* more than six. Nevertheless, to divide forms into those with six pairs perfect on the one hand and those with more than six (usually twelve or more) on the other, is on the whole a useful and reliable

distinction if used as one character among others, and fits in very well with what we may suppose the evolutionary history of the group to have been (see p. 487). The contrast between a typical form with six and a typical form with more than twelve

TEXT-FIG. 17.



Transverse section of body of *Sagartia miniata*. *APH.* Actino-pharynx. *APH.G.* Actinopharyngeal groove. *BW.* Body-wall. *D.* Directive mesentery. Numbers indicate mesentery-cycles.

pairs of perfect mesenteries is well shown by Text-figs. 18 (transverse section, *Calliactis parasitica*) and 17 (transverse section, *Sagartia miniata*), which also bring out the absence of any distinction into macro- and micromesenteries. In Text-fig. 17 most of the mesenteries of cycles 1 to 3 are seen to be perfect, and those which do not actually join

the actinopharynx in the figure do so in sections cut at a slightly higher level. Cycles 1 and 2 are almost indistinguishable at this level; cycle 3 is smaller, but all three cycles bear strong diffuse retractors (shown as black thickenings of the mesenteries), and their filaments and acontia are seen occupying the exocoels and endocoels as dotted patches.

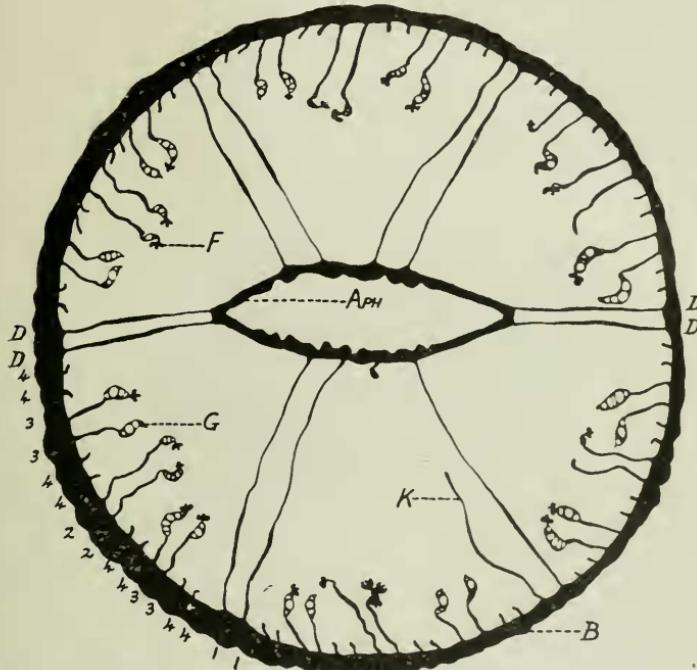
In Text-fig. 18 the primary mesenteries are certainly much wider than the others, but this particularly marked width is only found at the level of the actinopharynx where they stretch out to join it, and it is clearly seen that they have no strong musculature like the macrocnemes of *Phellia*, nor are they fertile. On the other hand, in this figure the mesenteries of cycles 2 and 3 bear weak retractors, filaments and gonads. In both Text-figs. 17 and 18 the fourth-cycle mesenteries are small at the level sectionised, being the youngest cycle in evidence at that level. In forms like this the mesenteries of the youngest cycle (sometimes even more of the youngest ones) are liable to remain small, and may sometimes be practically in the condition of *all* the imperfect mesenteries or microcnemes of a form where the distinction into macro- and microcnemes prevails. On the other hand they may become important as gonad-bearers.

In these forms which have lost the distinction into macrocnemes and microcnemes, the distribution of gonads is variable. They may be borne by all the mesenteries, or by all the older cycles, or the primary mesenteries may be sterile. In some cases, even, all but the *youngest* mesenteries are sterile. The distribution of reproductive organs is too variable within this group to be of any general use as a family character, but there are two well-marked families in which the gonads (Text-fig. 18) adopt one or other method of appearance exclusively. These two groups are the Chondractiniidae and Sagartiidae as limited on pp. 533 and 544. For further remarks on gonads see p. 517.

To turn to another character, most frequently anemones have the longitudinal muscle-layer of the tentacles borne upon more or less slender processes of the mesoglœa, which project outwards into the ectoderm and support the actual muscle-

fibres. This gives rise to a very characteristic appearance in a transverse section of a tentacle (or of the oral disc, the radial musculature of which generally resembles the longitudinal musculature of the tentacles), the outer edge of the mesogloea appearing fringed with little dendrites. The size,

TEXT-FIG. 18.



Transverse section of body of *Calliactis parasitica*. *APH.* Actinopharynx. *B.* Body-wall. *D.* Directive mesentery. *F.* Mesenterial filament. *K.* Interrupted perfect mesentery. Numbers indicate mesentery-cycles.

form and mode of branching of the latter varies according to species. Pl. 22, fig. 9, shows a typical example from *Sagartia miniata*.

In some genera, however, most of which on other grounds appear to be advanced, the longitudinal musculature of the tentacles and radial musculature of the disc have become

entirely embedded in the mesoglœa. It no longer has the form of branching processes bearing the fibres, but becomes a network of cavities the walls of which support the fibres (Pl. 22, fig. 8), or else the fibres merely lie in bundles in the mesoglœa. This state of affairs is obviously an advance on that in which the musculature is ectodermal, and is of a certain classificatory importance. There is not, it is true, any single family in which *all* the members present this feature, but in the Paractidae (in the strict sense, as defined on p. 548) it is so far the rule as to be of value in determining the relationships of the family. In a few cases the ectodermal type shows a partial sinking into the mesoglœa.

TEXT-FIG. 19.

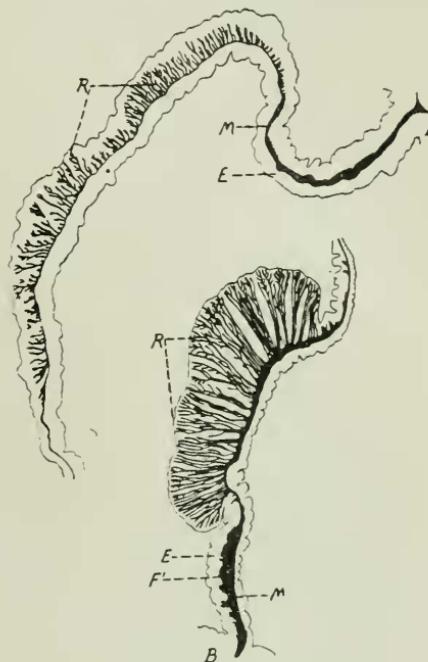


Transverse section of a part of body of *Actinauge richardii* showing part of body-wall and some mesenteries. *M.* Mesenterial filament. *R.* Retractor. Numbers indicate mesentery-cycles.

In some anemones the body is "all in one piece"—that is, not distinguished into definite regions. But in other cases three more or less well-marked zones are differentiated. These are seen at their best in *Edwardsia*, where the greater part of the body, or *scapus*, is marked off not only from the more delicate oral extremity (*capitulum*) which bears the tentacles, but also from the rounded vesicular aboral extremity or *physa*. In *Phellia* this distinction into three regions is also well marked. The *scapus* is corrugated and covered by a definite cuticle, and the more delicate *capitulum* is free from cuticle. Here the aboral end is really more a *physa* than anything else. Although it may be

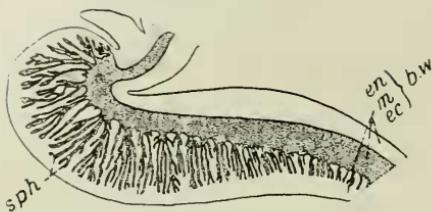
adherent it is more or less inflatable and is hardly as developed a pedal disc as is possessed by higher forms. In some other forms where a more definite pedal disc is present, the column may still be divided into a lower scapus provided with a cuticle as a rule, and an upper portion devoid of it. Although this upper portion does not exactly correspond with Gosse's meaning of the term "capitulum," since it is not particularly delicate in many cases, it would be rather confusing to give it another name, especially as the word "capitulum" has often been applied to it already. When a capitulum is present it can generally be introverted more or less into the scapus, and in such forms as *Phellia* and *Edwardsia* part of the scapus can be introverted also. I am using this series of characters as one among others in defining those families all the members of which conform to one type or the other. The basal extremity of the anemone may vary a good deal. Either it may be rounded and vesicular, as in *Edwardsia* and *Halcampa*—and then it constitutes a true physa—or it may form a definite and permanent pedal disc for adhesion, the

TEXT-FIGS. 20 AND 21.



Text-fig. 20 (Above).—Mesentery of *Aiptasia couchi*. Text-fig. 21 (Below).—Mesentery of *Sagartia miniata*. *B*. Body-wall. *E*. Endoderm. *F*. Short mesoglocal processes for muscle. *M*. Mesogloea. *R*. Retractor.

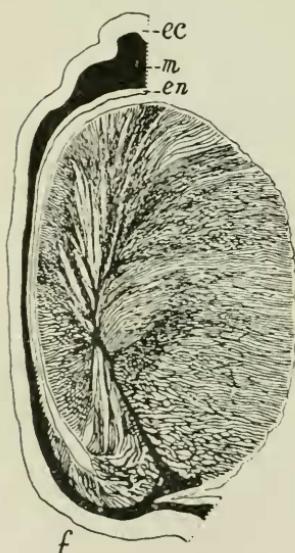
TEXT-FIG. 22.



Sphincter of *Bolocera longicornis*.
bw. Body-wall. *ec*. Ectoderm. *en*.
 Endoderm. *m*. Mesogloea. *sph*.
 Sphincter.

The Actiniina (i.e. those anemones which are outside the Stichodactylina, Edwardsiaria, Ceriantharia, and Zoanthinaria) seem to fall into two fairly well-marked groups according to the character of the marginal sphincter of the body-wall. The first group has this sphincter, if present, endodermal—that is to say, its fibres are supported on processes of the mesogloea which project into the endoderm. The endodermal sphincter may be diffuse (Text-fig. 22) or very much aggregated and circumscribed (Text-fig. 23).

TEXT-FIG. 23.



Sphincter of *Epiactis novozelandica*. *f*. indicates the fosse. Remainder as in Text-fig. 22.

is interesting to note that when special stinging organs are

pedal disc in some cases becoming concave and enclosing mud instead of adhering. There are, however, intermediates between true physa and true pedal disc. Some *Phellias* possess what is practically a physa, but may adhere. Further reference to this will be found at various points.

In the second group, which is the one directly dealt with in this paper, the sphincter has sunk entirely into the mesogloea, and the fibres become supported by the walls of cavities or lie in bundles in the mesogloea (Pl. 22, fig. 3).

In the group where the mesogloal sphincter is the rule, it

developed they are acontia, and not acrorhagi, etc.; nor are vesicles or pseudo-tentacles found within the group. Such structures as acrorhagi, vesicles and pseudo-tentacles occur freely among the forms with an endodermal sphincter (though of course by no means universally), and acontia do *not* occur in these 'forms.'¹ These are of course more differences of tendency than anything else, but they are interesting.

There are a few genera which possess acontia but have no sphincter at all. These I am including in the following discussions, with the forms which *have* the mesoglæal sphincter, because they agree with them in all other ways,

¹ With regard to the above paragraph, I would point out that although certain species have been recorded which do not agree with the statements I have made, the records are not in any case sufficiently certain, and need confirmation. If it should be found in the end that these records are accurate, it will involve certain modifications of my views, though not very fundamental ones. But for the present I prefer to leave doubtful genera out of account. The cases I refer to are those of *Nemactis* (a form said to have both acontia and acrorhagi), *Ophiodiscus* (please see note on this genus on p. 560) and certain genera described by Danielssen as possessing acontia and endodermal sphincters. Doubt has been thrown upon the anatomical work of the latter author, in some cases at all events, and it needs confirmation. One of the forms he describes as possessing acontia, and an endodermal sphincter is considered by Carlgren as a synonym of *Stomphia churchiae*, in which case it has neither. If *Aiptasia mutabilis* has really an endodermal sphincter it is possible that there is a special explanation of the endodermal sphincter in that particular case, as I shall show later on (p. 510). But as far as I can make out from Simon's description, it seems to me that what he is describing is not the true sphincter, but a secondary concentration of the endodermal circular muscle such as McMurrich and Hertwig have described in *Aiptasia* sp. ('Proc. Acad. Nat. Sci., Philad.,' 1889) and *Leiotealia nymphæa*. In both these species there is a true sphincter as well as and apart from the concentration of endodermal circular muscle in question, and the latter seems to be constricting the column to some extent, and is perhaps only temporary. It is not improbable that when living anemones constrict their bodies the endodermal circular muscle may form a temporary concentration. If this is the case in *A. mutabilis* it means that there is no true sphincter, which brings it into line with other *Aiptasia*-like forms.

and a study of them individually (carried out on p. 508) shows that they are clearly related to mesogloœal sphinctered forms.

Presence or absence of acontia and presence or absence of cinclides are characters which will be used, but I need not say more about them here as they have been fully discussed above. Generally speaking, we find a correlation between cinclides and a delicate body-wall always free from cuticle.

VI. A NEW METHOD OF GROUPING THOSE FORMS WHICH POSSESS EITHER ACONTIA OR A MESOGLOEAL SPHINCTER OR BOTH THESE CHARACTERS.

In studying various groups of the animal kingdom one is struck with the fact that it is possible to follow up, in some given group, a certain number of lines of evolution affecting certain organs or aspects of the animals in the group. It may happen that there are two or more alternative classifications of the group, which may express different lines of evolution, but which overlap and are not much correlated. The Lamellibranchs are a case in point. Attempts have been made to classify them on the basis of—

- (1) Gill structure.
- (2) Adductor muscles.
- (3) Hinge-lines and teeth.
- (4) Pallial lines and siphons.

It is possible to trace out what seem to be lines of evolution affecting each one of these aspects of the group, but when each of them is embodied in a separate classification there is overlapping and a certain lack of coherence. Each classification expresses the history of one organ or set of organs, but gives little clue to the probable history of the group as a whole.

It is a case which shows clearly that an ideal classification—that is, a classification expressing the history of the organisms of a group considered as wholes, cannot be built up around single characters, but must start upon the basis of the aggregate of the most important features of the animals

to be classified—that is to say, the sum of the more important characters should be used. Such a classification might hope to express the natural relationships of the whole animals as well as expressing the group-history as far as known, rather than the relationships and history of one isolated part of the structure.

This point of view is not only borne out but necessitated by the Mendelian discoveries, which show that any character or set of characters may have an independent hereditary history in the same series of organisms.

In the case of the Actiniina the application of this principle is badly needed. By a detailed study of the occurrence of acontia and of the mesoglœal sphincter in this group, Bourne has already shown that both these characters are too widely distributed through the group to imply any very close genetic relationship between the various forms possessing them, although, as I hope to show, in these particular cases there seems to have been a common ancestor. He has shown that we must dispose, once for all, of the idea that because two given forms possess acontia they must therefore be united in a single family. I have indicated this from my own point of view in my discussion of acontia and cinclides, and have endeavoured furthermore to show that the cinclis-character is not bound up with the acontium-character, and may be used independently. Whatever character be taken, it will be found that if it is attempted to build up families upon one or two characters only, the result is to bring together unrelated forms. No one would dream of uniting *Ophiodiscus* and *Halcampa* on the strength of the mesoglœal sphincter, or *Actinauge* and *Alicia* because both possess only six pairs of perfect mesenteries.

I hope to show that the families "Sagartiidæ" and "Paractiidæ," as at present understood, are in reality assemblages of more or less unrelated forms; that some genera belonging to one family are nearer certain genera of the other family than to those genera now classed with them; and that if we treat the Sagartid and Paractid genera as an unclassified series we

can build up from among them, on the basis of the sum of the more important characters, a number of very natural groups.

At this point, however, it is necessary to add a caution about the application of the sum-of-the-character principle. A certain amount of discrimination must be used in applying it. It may not be universally applicable, and it cannot in any case be used in a mechanical way like an arithmetical measure. The scheme will only give profitable results if a discrimination is made between those characters which are of primary importance and those which are of lesser value.

Characters of the latter class are those which are of value in distinguishing genera from each other, but cannot be introduced in considering families. Some of them are features which may have been independently acquired by two or more forms which are shown on the sum of more fundamental characters to be unrelated, in correlation with some similar but special mode of life (such as retirement to deep water) in the two cases. Opinions will naturally differ as to which are the most important characters, but in dealing with these anemones I have selected those which seem the most fundamental and least open to objection.

First of all let us consider the relationships of certain groups of genera.

1. *Marsupifer*¹ and *Phelliomorpha* share the following nine chief characteristics:

- (1) Column divided into scapus and capitulum.
- (2) Scapus provided with cuticle.
- (3) Mesenteries divided into macro- and microcnemes.
- (4) Number of macrocnemes limited to six pairs.
- (5) Pedal disc present.
- (6) Sphincter mesogloal.

¹ With reference to *Marsupifer* I propose to leave out of account the possession of brood-pouches by the female, as a special development, not of more than generic value at most for classificatory purposes. This character is one liable to occur anywhere in any family—cf. *Epiactis*. The double sphincter of *Marsupifer*, again, is a character peculiar to it as a *genus* only.

- (7) Longitudinal musculature of tentacles ectodermal.¹
- (8) Acontia absent.
- (9) Cinclides absent.

If we compare these genera with *Phellia* and *Decaphellia*, we find that the two latter genera have seven points (Nos. 1, 2, 3, 4, 6, 7, 9) in common with *Marsupifer* and *Phelliomorpha*, whereas the points in which the two pairs of genera differ from one another are only two in number, viz.—

- (1) *Phellia* and *Decaphellia* have acontia, *Marsupifer* and *Phelliomorpha* have not.
- (2) In *Phellia* and *Decaphellia* the base may be more or less a physa; in *Marsupifer* and *Phelliomorpha* a more definite pedal disc is present.

So far it is clear that *Phellia* and *Decaphellia* have so much in common with the other two genera that they must be considered as more or less related to them, though certainly not closely enough to be placed in one and the same family. Hitherto *Phellia*, etc., have been included in the *Sagartiidae* and *Marsupifer* in the *Paractidae*. It will therefore be advisable to examine their relationship to the typical forms of those families, i. e. *Sagartia* and its nearest relatives and *Paractis* and its nearest relatives.

The genera *Sagartia*, *Cerens* and *Artemidactis* have in common the following nine main features:

- (1) No division of the mesenteries into macrocnemes and microcnemes—the cycles are graded.
- (2) Number of perfect mesenteries exceeding six pairs usually exceeding twelve pairs.
- (3) Adherent base present.
- (4) Sphincter mesogloœal.
- (5) Acontia present.
- (6) Cinclides present.
- (7) Cuticle absent, body-wall fairly delicate.
- (8) Longitudinal muscles of tentacles ectodermal.
- (9) Primary mesenteries fertile as well as others.

¹ This is the rule. Rarely a *part* of the musculature is enclosed by anastomosis of the mesogloœal processes which project into the ectoderm.

Of these nine characters, Nos. 3 (more or less), 4, 5, 8 recur in *Phellia* and *Decaphellia*. Character 9 is not applicable to them, because although their primary mesenteries are fertile no others are, all the others being microcnemes. The *Phellia* group, then, has four characters in common with the *Sagartia* group, and five points of difference. But we have already seen that the *Phellia* group has seven features in common with *Marsupifer*, etc., so it is evident, not only on this account but also because of the large number of differences between the *Phellia* and *Sagartia* groups, that *Phellia*, etc., are more closely related to *Marsupifer*, etc. (hitherto classed as "Paractid"), than to *Sagartia*, etc. But since *Phellia* and *Marsupifer*, although fairly nearly related, are not near enough to each other (for the differences see above) to be classed in the same family, it is clear that *Phellia* and *Decaphellia* must be separated from the *Sagartia* group and classed as a separate family. Bourne has listed the characters of the *Phelliidae* (10, p. 78) in a slightly different way, and has shown clearly that of thirteen characters especially distinguishing them, no less than ten are found also in *Halcampa* (which differs from *Phellia* in so far as it lacks acontia and cuticle and possesses cinclides). Of Bourne's thirteen characters only two (presence of acontia and a mesogloœal sphincter) are present in *Sagartia*, whereas *Phellia* and *Sagartia* show eleven points of difference. From this it is seen that *Phellia* has so much more in common with *Halcampa* than with *Sagartia* that it must be placed in a separate family from the latter, near the *Halcampidae*. Bourne therefore claims family rank for the group containing *Phellia* and *Decaphellia*, and I have given additional evidence for the necessity of this by comparing them with *Marsupifer* and *Phelliomorpha*, which are their near relations on a different side from *Halcampa*. It now remains to compare *Marsupifer*, etc., with those forms most typical of the *Paractidae*.

The genera *Paractis*, *Cymbactis*, *Hormosoma*, *Actinostola*, *Catadiomene* and *Stomphia*, the forms in

question, share four of the characters listed on p. 470 for *Marsupifer*, etc. (Nos. 5, 6, 8, 9), but differ from the *Marsupifer* group as regards characters 1, 2, 3, 4 and 7, some of which are most fundamental characters affecting the mesenteries.

If, therefore, *Marsupifer*, etc., agree with *Phellia*, etc., as regards seven characters (and disagree in two), whereas they only agree with the typical Paractids in four and disagree in five respects, they have clearly more in common with *Phellia* than with *Paractis*, and cannot therefore be included in one family with *Paractis*. But since they are at the same time *sufficiently* different from *Phellia* to claim family distinction, they must be placed in a group of their own.

Another group of forms which will afford us a good example is that which contains the genera *Diadumene*, *Pelocetes*, *Phytocetes*, and *Mena* (Pl. 22, figs. 12, 13, Text-fig. 28). These four genera have seven important common characters:

- (1) Mesenteries divided into macrocnemes and microcnemes.¹
- (2) Number of macrocnemes limited to six pairs.
- (3) Acontia present.
- (4) Cinclides present.
- (5) A definite base present which may be reduced and physa-like.
- (6) Body-wall delicate and devoid of cuticle.
- (7) Longitudinal musculature of tentacles ectodermal.

Sphincter usually absent, but may be mesoglœal.

These forms (the *Diadumene* group) share characters 1, 2, 4, 6, 7 with *Halcampa*, from which they chiefly differ by the possession of acontia and a definite base; but even the latter may be reduced in connection with a burrowing life.

Secondly, the *Diadumene* group shares characters 1, 2, 3, 5 and 7 with the *Phelliidae* (*Phellia* and *Decaphellia*), from which it differs in that its members possess cinclides but no cuticle and no division of the body into scapus and capitulum.

¹ This character being somewhat violated by *Diadumene*.

Thirdly, the Diadumenids share characters 3, 4, 5, 6, 7 with the *Sagartia*-*Cereus*-*Artemidactis* group, but differ from the latter fundamentally as regards the mesenteries.

From this it is evident that—

- (1) These forms are as closely related to *Halcampa* and *Phellia* as to *Sagartia*, and cannot therefore be classed with the latter. (If they are carefully studied they really seem nearest of all to *Halcampa*.)
- (2) Since they are equally related to three other different sets of genera, but not quite closely enough to any one of the latter to be included in the same family (see differences noted above) with them, they must obviously be established apart as a family distinct from either of the other three sets.

A last example may be taken by comparing the genera *Actinoscyphia*, *Isoparactis* and *Paranthus* with certain other groups of genera.

The three genera mentioned have the following seven important common characters:

- (1) Primary mesenteries grade into secondaries, secondaries into tertiaries, etc., so that there is no division into macrocnemes and microcnemes.
- (2) Number of perfect mesenteries limited to six pairs.
- (3) Pedal disc present.
- (4) Sphincter mesoglœal.
- (5) Acontia absent.
- (6) Cinclides absent.
- (7) Longitudinal musculature of the tentacles ectodermal.

The Paractis group possess characters 1, 3, 4, 5, 6 of the above list, and a few of them also No. 7. The chief difference is that the Paractids have numerous perfect mesenteries, the Actinoscyphids only six pairs, added to which the majority of forms related to *Paractis*, including all those referred to above as its most typical relatives, have the longitudinal musculature of the tentacles embedded in the mesoglœa.

The large group of genera containing *Actinangle*, *Chondrodactis*, *Hormathia*, *Paraphellia*, etc.—i.e. the Chondractiniinæ of Haddon—possess *all* the characters above mentioned for *Actinoscyphia*, etc., except that they have acontia (which may be rudimentary).

Consequently *Actinoscyphia* and its relations have more in common (six features) with, and less to separate them from (one feature), the Chondractiniinæ than they have with the Paractids with which they have so far been classed. But the absence of acontia is enough to separate them from the Chondractiniinæ, and I have simply introduced the comparison to show that they cannot be included with *Paractis*, etc., when they are even more related to another set of forms than they are to that. So *Actinoscyphia*, etc., must also constitute a distinct family.

The above analysis brings out several facts. It shows that “*Sagartiidæ*”, and “*Paractidæ*” as they stand are both families containing a wide series of forms, the extremes of which are so much separated that it is impossible to place them in one and the same family on the strength of one or two resemblances only. It is quite imperative, for instance, to separate the *Phellia* group and the *Diadumene* group from *Sagartia* and its nearest relatives, and the *Marsupifer* group and the *Actinoscyphia* group from *Paractis* and its allies. It is also seen that some “*Sagartids*” (e.g. *Phellia*) are more closely related, considered on the sum of the principal features, to certain “*Paractids*” (e.g. *Marsupifer*) on the one hand, and to *Halcampa* on the other, than they are to other “*Sagartids*.” Clearly the families “*Sagartiidæ*,” “*Paractidæ*” and “*Halcampidæ*” are so much inter-related that they no longer represent an adequate classification, and must be broken up. We can no longer define two groups as “*Actiniina* possessing acontia” (“*Sagartiidæ*”) and “*Actiniina* possessing a mesogloœal sphincter and a pedal disc but no acontia” (“*Paractidæ*”), because that arrangement is now seen to be unnatural and insufficient.

If, therefore, we treat all the Paractid and Sagartid genera as a completely unclassified series for the moment, and apply to them the principle of the sum of the most important characters, we shall find that we can build them up into a number of eminently natural groups. Each of these groups will represent a collection of genera clearly defined on the basis of the possession of a sufficient number of the most important common characteristics, and as such will rank as a family. Each family will present at least six, generally seven or eight or nine, features of importance common to all its members. I will enumerate these families without further discussion, and comment upon them afterwards. In splitting up the "Sagartiidae" and "Paractidae," I have, of course, retained those two names for that group of genera which may be considered most typical in each case, i.e. *Sagartia* and its nearest relations in the first case, and *Paractis* and its closest relatives in the second.

1. DIADUMENIDÆ.

The genera *Diadumene*, *Mena*, *Pelocetes* and *Phytocetes* form this family, and have in common the following seven characters:

- (1) Mesenteries divided into macrocnemes and microcnemes, the division not fully expressed in *Diadumene*.
- (2) Number of macrocnemes limited to six pairs.
- (3) Acontia present.
- (4) Cinclides present.
- (5) A definite base present which may be reduced and physa-like.
- (6) Body-wall delicate and devoid of cuticle.
- (7) Longitudinal musculature of tentacles ectodermal.

Sphincter usually absent, but may be very weak mesogloëal.

2. PHELLIIDÆ.

Genera: *Phellia*, *Decaphellia*, *Halcampactis*. Number of common characters, 8.

- (1) Body divided into scapus, capitulum, and base or physa, which may adhere.
- (2) Scapus provided with a cuticle.
- (3) Mesenteries divided into macro- and microcnemes.
- (4) Maximum number of macrocnemes six pairs.¹
- (5) Capitulum and upper third of scapus can be introverted.
- (6) Acontia present.
- (7) Cinclides absent.
- (8) Longitudinal musculature of tentacles ectodermal or rarely partly enclosed by anastomosis of ectodermal processes of mesoglœa.

Sphincter mesoglœal in *Phellia* and *Decaphellia*, possibly also in *Halcampactis*; or if not, absent.

3. MARSUPIFERIDÆ.

Genera: *Marsupifer* and *Phelliomorpha*. Number of common characters, 9.

- (1) Body divided into scapus and capitulum.
- (2) Scapus provided with a cuticle.
- (3) Mesenteries divided into macrocnemes and microcnemes.
- (4) Number of macrocnemes limited to six pairs.
- (5) Pedal disc present.
- (6) Sphincter mesoglœal.
- (7) Acontia absent.
- (8) Cinclides absent.
- (9) Longitudinal musculature of tentacles ectodermal.

4. METRIDIIDÆ.

Genera: *Metridium*, *Calliactis*, *Adamsia*, *Aiptasia*, *Aiptasiomorpha*, *Heteractis*, *Bartholomea*. Number of common characters, 7.

- (1) Cycles of mesenteries grading into each other, so no division into macrocnemes and microcnemes is present.
- (2) Number of perfect mesenteries limited to six pairs or a very few more.

¹ Or in exceptional instances a very few more.

- (3) Pedal disc present.
- (4) Acontia present.
- (5) Cinclides present.
- (6) Cuticle absent; body-wall usually more or less delicate.
- (7) Longitudinal musculature of tentacles wholly or partly ectodermal.

Sphincter mesoglæal except in Aiptasiomorpha and Bartholomea, where it is absent.

5. CHONDRACTINIIDÆ.

Genera: *Hormathia*, *Actinauge*, *Chondrodactis*, *Paraphellia*, *Sagartiomorphe*, *Leptoteichus*. Number of common characters, 8.

- (1) Cycles of mesenteries grading into each other, so no division into macrocnemes and microcnemes is present.
- (2) Number of perfect mesenteries limited to six pairs or a very few more.
- (3) Pedal disc present.
- (4) Acontia present.
- (5) Cinclides absent.
- (6) Longitudinal muscles of tentacles partly or wholly ectodermal.
- (7) Primary mesenteries always sterile.
- (8) Sphincter mesoglæal.

6. ACTINOSCYPHIIDÆ.

Genera: *Actinoscyphia*, *Paranthus*, *Isoparactis*. Number of common features, 7.

- (1) Cycles of mesenteries grade into one another, so there is no division into macrocnemes and microcnemes.
- (2) Number of perfect mesenteries limited to six pairs.
- (3) Pedal disc present.
- (4) Sphincter mesoglæal.
- (5) Acontia absent.
- (6) Cinclides absent.
- (7) Longitudinal musculature of tentacles ectodermal.

7. SAGARTIIDÆ (in a much more restricted sense than hitherto).

Genera : *Sagartia*, *Cereus*, *Artemidactis*. Number of common characters, 9.

- (1) Cycles of mesenteries grading into one another, so that no division into macrocnemes and micronemes is present.
- (2) Number of perfect mesenteries exceeding six pairs, usually exceeding twelve pairs.
- (3) Primary mesenteries fertile as well as others.
- (4) Cuticle absent; body-wall fairly delicate.
- (5) Cinclides present.
- (6) Acontia present.
- (7) Sphincter mesoglæal.
- (8) Longitudinal musculature of tentacles ectodermal.
- (9) Pedal disc present.

8. CHORIACTIDÆ.

The genus *Choriactis* stands alone. Perhaps *Mitactis* and some other forms will go with it when better known. Its chief characteristics are :

- (1) Cycles of mesenteries grading into one another so that no division into macrocnemes and microcnemes is present.
- (2) Number of perfect mesenteries considerable.
- (3) Pedal disc present.
- (4) Sphincter mesoglæal.
- (5) Acontia present.
- (6) Cinclides absent.
- (7) Wall may be thick; no cuticle.
- (8) Longitudinal musculature of tentacles ectodermal.

9. PARACTIDÆ (in a much more restricted sense than hitherto).

Genera : *Paractis*, *Cymbactis*, *Stomphia*, *Hormosoma*, *Alloactis*, *Actinostola*, *Catadiomene*, *Poly-siphonia*, *Ophiodiscus*, *Sicyonis*, *Antholoba*, *Parantheoides*, *Tealidium*. Number of common features, 6 and a seventh not quite universal tendency.

- (1) Cycles of mesenteries grading into each other, so no division into macrocnemes and microcnemes is present.
- (2) Numerous mesenteries perfect.
- (3) Sphincter mesoglœal.
- (4) Acontia absent.
- (5) Cinclides absent.
- (6) Pedal disc present.

In *Paractis*, *Cymbactis*, *Stomphia*, *Hormosoma*, *Actinostola*, *Catadiomene*, *Polysiphonia*, *Ophiodiscus*, *Sicyonis*, the longitudinal musculature of the tentacles and radial musculature of the oral disc is entirely embedded in the mesoglœa. In *Antholoba* and *Alloactis* it is partially so.

It will be observed that in all the families enumerated above there are forms possessing a mesoglœal sphincter and that in six of the nine all forms have it. In the three families where there are exceptions these exceptional genera agree in all other respects with the other members of their families which *do* possess the sphincter and are bound to be classed with them on the sum of the characters. We may, therefore, fairly consider the mesoglœal sphincter as a character common to all nine families which has been lost in a few special cases, probably in correlation with some special form of life. This probability is more fully discussed in connection with the individual sphincterless genera on p. 508. *The presence of the mesoglœal sphincter is the only character common to all families*, apart from the fact that some sort of definite base is usually developed, and even this may be physa-like.

The sphincter apart, it will be noted that there are a number of other characters, presence or absence of which determine the limits of the groups. Some of these occur in such a regular manner that it will be worth while to consider them in tabular form. The characters to which I refer are :

- (1) Presence or absence of acontia.
- (2) Presence or absence of cinclides.

	Aconzia present. Cinclides present.	Aconzia present. No cinclides.	No aconzia. No cinclides.
Mesenteries divided into macrocnemes and microcnemes. Number of macrocnemes typically six pairs at most.	Diadumenidae. Diadumene. Pelocetes. Phytocetes. Mena.	Phelliidae. Phellia. Decaphellia. Hacampactis.	Marsupiferidae. Marsupifer. Phelliomorpha.
Mesenteries <i>not</i> divided into macrocnemes and microcnemes. Number of perfect mesenteries six pairs or rarely a very few more.	7. Metridiidae. Metridium. Callactis. Aiptasia. Aiptasiomorpha. Actinia. Heteractis. Bartholomea.	8. Chondractiniidae. Actinangle. Hormathia. Chondrodactis. Leptoteichus. Sagartiomorpha. Paraphelia. ? Phelliactis.	9. Actinosecyphidae. Actinosecyphia. Paranthus. Isoparactis. ? Lilliella.
Mesenteries <i>not</i> divided into macrocnemes and microcnemes. Number of perfect mesenteries exceeding six pairs, usually exceeding twelve pairs.	7. Sagartiidae. Sagartia. Cerens. Artemidactis.	8. Choriactidae. Choriactis. ? Mitactis.	7. Paractidae. Paractis. Hornosoma. Stomphia. Actinostola. Ophiodesmus. Polysiphonia. Antholoba.
			8. Parantheoides.
			6.

In this table the number in the corner of each square is the number of characters which the members of the family in that square have in common.

(3) Presence or absence of a sharp division of the mesenteries into macrocnemes and microcnemes.

(4) Limitation of number of macrocnemes, when macrocnemes are present, to six pairs, or absence of this limitation.

(5) Presence or absence of any considerable number of perfect mesenteries over and above the six primary pairs in forms where the distinction between macrocnemes and microcnemes has been lost.

In the above table one square is given up to each family; the characters printed at the head of each of the three vertical columns apply to all three of the squares in that column. The characters printed at the side of the table apply to the three families on a horizontal level with them. So one can arrive at the four main points about any one family by combining the two points at the head of the vertical column containing that family with the two points on a level with the square occupied by it.

From this it will be seen that—

(1) Among those three families in which acontia and cinclides occur all three kinds of mesenterial development are found: the first, where there are six pairs of macrocnemes and all other mesenteries are microcnemes; in the second, where there is no distinction into macro- and microcnemes, but where only six pairs are perfect, in the Metridiidae; and the third, similar to the second but with numerous perfect mesenteries, in the Sagartiidae.

(2) Among the three families in which there are acontia but no cinclides, *the same three types of mesenterial arrangement occur*—the first in the Phelliidae, the second in the Chondractiniidae, and the third in the Choriactidae.

(3) The same remarks apply to the three families in which acontia and cinclides are both absent. Here the first type of mesenterial arrangement is found in the Marsupiferidae, the second in the Actinoscyphiidae, and the third in the Paractidae.

4) If we were to start from another point of view we should find among those forms which possess the division of

mesenteries into macro- and microcnemes some forms with acontia and cinclides (*Diadumenidæ*), some with acontia and no cinclides (*Phelliidæ*), and some with neither the one nor the other (*Marsupiferidæ*). If we took, again, either those forms in which there is no division into macro- and microcnemes, but which have six pairs of mesenteries alone perfect, or those in which numerous pairs are perfect, we should find that in each case some of them had acontia + cinclides, some acontia and no cinclides, and some no acontia and no cinclides.

This shows that if we begin to build up families founded on mesentery-characters only, each one will include forms with acontia and cinclides, forms with acontia only, and forms with neither one nor the other, which is out of the question. Again, it is equally out of the question to found families on acontium- and cinclis-characters only, since then each family would include forms presenting fundamentally different types of mesenterial arrangement. It is therefore evident that we must use, not mesentery-characters only nor acontium-and-cinclis-characters only, but both in combination. Other characters may be brought in as well.

In this way the conclusion is reached that the nine sets of forms enumerated above as groups of genera clearly defined on the basis of the sum of their most important characters, and *not subordinate to other modes of grouping*, rank as families. The possibility of including all nine groups in *one* family, defined by the sole common character of the possession of a mesogloea sphincter, thus bringing together a host of forms with widely separated extremes, is too far from the mark to need discussion.

The nine families thus established are more fully defined on pp. 520-564. The discussion of their probable evolutionary history which follows will, I hope, give the arrangement an intelligible meaning.

It is, perhaps, worth noting that a number of these nine families have been in existence already as subfamilies. These are the *Phelliidæ*, *Metridiidæ*, *Chondractiniidæ* and *Sagar-*

tiidæ in the new sense. These have long been recognised as natural groups, but apart from them the allocation of forms has been unsatisfactory.

Before going on to discuss the evolution of the forms included in these families, it is necessary to speak of a form which I have not included in any one of them, and which I only found after most of the work for this paper was done. This form is one having the general appearance of a large *Phellia*, and it is near Carlgren's *Isophellia*; but till more is known of both *Isophellia* and of my form, it is not possible to assume their identity, and I have given mine the name *Flosmaris*. A short description of it will be found on pp. 441-443, and I give here a generic definition of it so that there will be a proper basis for discussion.

Flosmaris, n. gen.

Basal disc present. Body divided into a long scapus and a short capitulum; lower part of scapus may be very thin-walled. Main part of scapus with numerous small papillæ which attach sand-grains. Capitulum fairly smooth, devoid of sand, its margin tentaculate. Tentacles simple, their longitudinal musculature ectodermal. Sphincter rather small, confined to upper part of capitulum. Mesenteries sharply divided into macrocnemes and microcnemes. Twelve pairs of fully developed macrocnemes bearing gonads, circumscribed retractors and filaments, and all perfect. The other mesenteries are microcnemes and consist chiefly of a parietal muscle. Acontia present. Cinclides probably absent.

Species: *F. phellioides*, n. sp.

If reference be now made to the table of squares on p. 481, it will be seen that the squares actually shown in the table do not represent every *possible* combination of the characters placed at the heads and sides of the columns. They represent, however, every combination of these characters which is actually represented by hitherto-described anemones, with the one exception of *Flosmaris*.

If one were to construct a table showing every possible

combination of the characters used, the number of squares would be not nine but sixteen. We should have one additional vertical column for forms with cinclides but no acontia, and one additional horizontal column for forms with the mesenteries divided into macrocnemes and microcnemes, but with the number of macrocnemes twelve or more pairs instead of six pairs.

I have not actually included the additional squares which would result from adding these two other possible columns, because as yet too little is known of any possible forms which might fill them to make it safe to do so. But Actiniaria are unexpected creatures, and one finds that new combinations of characters *do* turn up among them. It is therefore not at all impossible that some forms may occur and be discovered in the future which will fill some or all of the squares not covered by the nine already filled. *If this should happen, I claim that on the same grounds which make each of the nine known families valid, it will be necessary to erect further families until the limit of the possible combinations of the four characters in question be reached.* If forms representing new combinations should simply be allocated to the one of the nine already known families to which they happen to be nearest, it would eventually widen the limits of those families too much, and cause confusion, and each family would cease to represent an evolutionary stage or a natural group. It may be objected that a great multiplication of families is involved if all combinations are to have their due; but this is not really a valid criticism, because the arrangement of having a fairly large number of comparatively small and exactly-defined families is actually a very convenient one, and facilitates identification, quite apart from the fact that it gives more chance of having homogeneous and natural groups and representing relationships of whole animals and not parts of animals by them.

To apply all this to *Flos maris*. *This species does actually represent one of the hitherto unrecorded combinations not included in the table.* It represents the combination of

acontia and (probably) no cinclides with the division of the mesenteries into macrocnemes and microcnemes, but with twelve pairs of macrocnemes and not six pairs as in the Phelliidæ. It comes fairly close to *Phellia* of course, but one may claim separation for it on the same grounds as those on which the Sagartiidæ, Choriactidæ and Paractidæ are separated from the Metridiidæ, Chondractiniidæ and Actinoscophiidæ.

Flosmaris, therefore, is the type-genus of another new family, the Flosmarinidæ, which will be characterised by the main features of its type-genus.

For the present, however, I do not wish to insist too much on this family Flosmarinidæ, but I simply establish it tentatively pending further knowledge. I do this because the type-genus is as yet known only from one single specimen, and until more come to hand one can never be sure that there is not something abnormal about a solitary individual. However, I am inclined to think it is really genuine and not abnormal; it is a beautifully regular and well-developed specimen, and well preserved. It might be suggested that it is an overgrown *Phellia* which has doubled its organs. This is possible of course, but nevertheless it would be curious, because some genuine *Phellia*s as large as *Flosmaris* still retain only six pairs of macrocnemes, the other mesenteries remaining small. The point cannot be finally settled as yet.

The remaining question is, whether any other combinations hitherto unrecorded are likely to come to hand beside the Flosmarinidæ combination. Of course no one knows, but it does not seem at all unlikely that some of them at any rate will do so. It would not be surprising, for instance, if forms bearing the same relation to the Diadumenidæ and Marsupiferidæ as *Flosmaris* does to the Phelliidæ (i. e. with the same combination of acontia and cinclides as those families, but with twelve or more instead of only six pairs of macrocnemes) should be recorded sooner or later. With regard to the other possible combinations—all three involving forms with a mesogloal sphincter and probably a pedal disc but

with cinclides and no acontia—it seems much less likely, from one's general ideas about the group, that these exist, but of course they may do so.¹ Some forms about which little is known, and which I have not assigned to a definite position in this paper, are *Stephanactis* and *Amphianthus*. The former as described by Hertwig has cinclides but no acontia, and may possibly represent one of the other combinations. I have some specimens of *Stephanactis* which I may be able to describe sooner or later in connection with this.

With regard to *Isophellia*, it is hardly yet possible to form a final opinion. *I. sabulosa* is described by Carlgren (1900, p. 72) from a single specimen, and this specimen seems intermediate between *Phellia* and *Flosmaris* in that it has three extra couples of macrocnemes in addition to the six primary pairs. And even some at least of the remaining weaker mesenteries of the second cycle seem to have some of the characters of macrocnemes. Only further material will make us certain whether it is an unusual and exceptional member of the *Phelliidae* or a not quite fully developed example of the *Flosmarinidae*. I think the latter is quite possible. For the present, therefore, I have placed it with a query in the *Phelliidae*, and it can easily be removed if the family *Flosmarinidae* makes good, and if it really belongs there.

A further note with regard to the position of *Flosmaris* and of any further possible combinations in my evolutionary scheme will be found on p. 507.

VII. SUGGESTIONS CONCERNING THE EVOLUTIONARY HISTORY OF THE FORMS WITH ACONTIA OR A MESOGLOEAL SPHINCTER OR BOTH.

I should like to make it clear that the nine families outlined above (and defined later) are not dependent for their validity

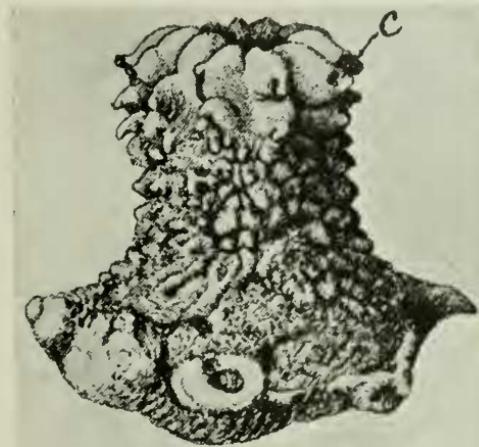
¹ *Halcampa*, of course, has a mesogloal sphincter and cinclides but no acontia, but this comes rather outside the scope of the present paper, and is probably fairly near the ancestor of all the forms here discussed. See evolutionary arguments.

upon the acceptance or otherwise of the following suggestions. They seem to represent the only natural grouping in any case, but the evolutionary scheme which will be developed below renders the arrangement more intelligible, and appears to fit the facts of the case.

In endeavouring to work out some idea of the way in which these forms evolved from a common ancestor, the first step is no doubt to try to decide fairly which of the nine families contains the most primitive forms. In order to do this it is necessary to find out what characters are primitive, and perhaps the best way to do this would be to compare some fairly primitive form with an advanced one. Two convenient ones would be *Halcampa chrysanthellum* and *Catadiomene atrostoma*. I select these two simply because they illustrate my meaning well, but others might be substituted for them with slight alterations. I imagine it will be generally admitted that *Halcampa* is a fairly primitive form. It is more advanced, of course, than *Protanthea*, *Edwardsia*, etc., but still is near enough to the ancestral form of the majority of the *Actiniina* to serve our purpose. I do not wish to go too far back, since I am discussing the evolution of one portion of the *Actiniina*, not of the whole of the *Actiniaria*. What claim has *H. chrysanthellum* to primitiveness? It is small, and its body-wall is delicate and perforated by pores. It is not very different from a certain stage of larval development through which most *Actiniina* pass, and which may be called the *Halcampa* stage. Its mesenteries are few in number and its sphincter is weak. The longitudinal musculature of the tentacles has not sunk into the mesogloea. Its base is a physa, and it has developed no pedal disc or differentiated basilar and parieto-basilar muscles. On the other hand, what claims has *C. atrostoma* as an advanced form? It is a large animal with a well-defined pedal disc, and in correlation with this a sharp differentiation of basilar and parieto-basilar muscles. It seems to have taken to deep-water life, and, as in many other deep-water animals, it has developed a thick body-wall devoid of pores, and has lost

mobility. The body-wall has also a certain development of knobs and crests (not as conspicuous here as in some other cases, cf. Text-fig. 24, which shows knobs and crests in *Actinauge*, and Text-fig. 25, which shows knobs in *Chondrodactis*), and at the base of every tentacle, on the outer side, is a solid mesoglœal swelling. These are all points which seem to me to indicate an advanced stage of evolution. What is the reason for them? The thick body-wall, the knobs and

TEXT-FIG. 24.



Actinauge richardi. c. Capitulum.

crests and tentacular swellings are found in a number of anemones which appear to be advanced forms. They may be partly protective, but we need not lay too much stress on that aspect of them, because they do not seem efficient enough to act as any great deterrent to such an enemy as a determined fish, for instance. There are other deep-water anemones, and successful ones to all seeming, which have surprisingly delicate body-walls (e. g. *Bolocera longicornis*). On the other hand, the spreading of an anemone to a deep-water habitat is probably a change towards a slower

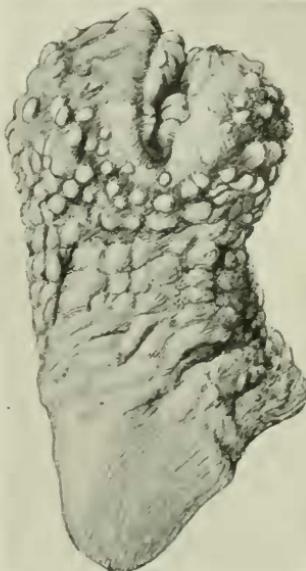
metabolism. We know that there are curiosities of respiration, for instance, in the molluscs Pleurotomaria and Lepeta, which apparently have slow metabolism. The marked uniformity of low temperature in deep water may be connected with low metabolism and respiratory difficulties. If the ratio of anabolism to katabolism changes value, there is energy to spare which may be used up in decoration, and I am inclined to regard the knobs, etc., of deep-water anemones in this light. They do not seem to be features which can have any great importance to the animal in its life, save that increased thickness of body-wall means a certain loss of mobility, and is therefore detrimental rather than otherwise. It would not be altogether out of place to compare the basal swellings, crests, etc., of these anemones (especially of *Actinnauge*) with the knobs and spines developed by such groups as Dinosaurs and Ammonites in the late phases of their evolution. It is not impossible that they indicate a last phase in the evolution of these anemones, especially if we consider that the deep sea is a refuge and that the forms possessing them are becoming somewhat less active and are advanced in other ways. Nevertheless, I suggest it with reserve as a mere possibility.

To get back to *C. atrostoma*, it has other characters giving it claim to an advanced condition. The longitudinal musculature of the tentacles and radial musculature of the oral disc are entirely embedded in the mesogloea, and this is obviously an advance on the condition in which that musculature is ectodermal. If we take all the cases of *Actiniine* anemones in which this embedded musculature occurs, whether they have mesogloal sphincters or not, we find that they are all forms with *numerous perfect mesenteries*,¹ i. e., it never occurs in forms in which the number of mesenteries perfect is limited

¹ I am not aware of any exception to this among the forms where the musculature is truly and entirely embedded. There are cases in which the ectodermal musculature tends to be partly embedded at its base (meso-ectodermal) in which the rule does not apply, but these are rather different.

to six pairs, or in which the division into macrocnemes and microcnemes is found. This seems to suggest that, since forms with the embedded tentacular musculature must at all events be moderately advanced, the condition with numerous perfect mesenteries is also an advance on the state where few are perfect. *C. atrostoma* has a very large number of mesenteries, and not only are many of them perfect, but the primaries are sterile. Lastly, the sphincter is well developed. If we assume for the moment that the characters I have enumerated for *Halcampa* are primitive, and those for *Catadiomene* advanced, I believe there is a reasonable way in which we can account for their being so. It seems to me to be a tendency of Actiniaria in general, broadly speaking, to specialise in size of the individual, and perhaps more especially in diameter. The small size and worm-like form of *Halcampa* are not adapted to the possession of many mesenteries. It seems reasonable to suppose that, starting from small forms with few mesenteries, if we get increase in size (especially diameter) we may expect a correlated multiplication of organs, i. e. increase in the number of mesenteries. Again, if the mesenteries were at first few in number they would have to do all the work, and primitively they were no doubt all alike, division of labour coming later on with increase in number. This being so we should expect that each mesentery would bear a strong retractor muscle, a gonad, and a filament. This is actually the case in certain fairly

TEXT-FIG. 25.



Chondrodactis duplicata.

primitive forms (e. g. some species of *Halcampoides*). New mesenteries when they appeared would at first be narrow and rudimentary (perhaps until there was more room for them); and we find that our *Halcampa* represents this stage, having six pairs of large macrocnemes to do the work and a few very small microcnemes which take no share. As evolution progressed the new small mesenteries would tend to increase in size and importance, and take over some of the work from the primaries. The primaries would need less powerful musculature, since they would have the aid of the secondaries in the work of retraction, and their muscles would tend to become less individually specialised. In *Halcampa* we find, therefore, excessively strong muscles on the few macrocnemes, in *Catadiomene* less strong diffuse ones on all the older mesenteries. With the increase in size and number of the secondary mesenteries, the growth of the primaries would tend to become fairly complete before the animal approached the adult condition. The production of gonads is usually from tissue which has retained a more or less embryonic condition, and would therefore be more likely to occur in the newer and still growing mesenteries than in the older perfect ones. This should not be taken to imply any suggestion that no increase in size takes place after the appearance of gonads, but rather that the appearance of gonads on younger mesenteries, broadly speaking and with some exceptions, seems to indicate that the process of differentiation has passed its climax in the oldest mesenteries.

All this assumption of importance by the secondary mesenteries would mean that the sharp distinction which is present in forms where they are rudimentary into the original large macrocnemes and a number of small microcnemes would be gradually lost. There would then be several cycles of well-developed mesenteries grading off into each other, and all the older ones would bear retractors and filaments. The tendency would be for the primaries to become sterile. At first the primary mesenteries, which represent the original macrocnemes, would still so far predominate over the others.

that they alone would be perfect. But in the end the secondary and tertiary mesenteries would join the actinopharynx also, and a form with numerous perfect mesenteries would be attained.

The increase in size of the mesogloal sphincter is an obvious advance, in working from a small form to a larger one. I will refer in more detail to the evolution of a pedal disc shortly.

Other anemones, generally looked upon as fairly primitive, present features broadly similar to those of *Halcampa*. Opinion will naturally differ as to which are primitive, but it seems safe to suppose that *Gonactinia*, *Protanthea* and probably *Oractis* form one primitive group, and the *Edwardsias* another. *Halcampa* and *Halcampoides* represent a step onwards, and then there are the probably rather more advanced but still fairly primitive genera *Pentactinia*, *Peachia*, *Haloclava* and *Eloactis*. There is also the genus *Harenactis*—rather an unusual one.¹

The *Gonactinia*-*Protanthea* group (probably including *Oractis*) must be considered apart from the others as perhaps representing survivals of the earliest anemones of all, which have developed in some directions and remained primitive in others. Their primitive traits are their small

¹ While referring to the group of anemones mentioned here, it would perhaps be as well to mention that the group "Ilyanthidae" to which they belong will need splitting up if the principles set forth in this paper be accepted. I am not yet in a position to suggest any detailed classification of the Ilyanthidae; but I should like to mention one or two points about them. In the first place it seems that *Halcampa* and *Halcampoides*, and possibly others with them, will form one natural group, the *Halcampidae*. Secondly, *Ilyanthus* is a genus containing two forms which are widely different from each other, and each of which needs separate consideration from the rest of the "Ilyanthidae." It is not impossible that *I. mitchelli* and *I. parthenopeus* may even be allocated to different families. With regard to the rest of the forms under discussion, *Peachia* and others, judgment must be reserved at present. The ground for the splitting will not, however, be solely the character of the sphincter muscle, but the sum of the main characters.

size, weak and somewhat generalised musculature (surviving even in the body-wall ectoderm), and the presence of only eight perfect mesenteries corresponding to the macrocnemes of *Edwardsia*. They have an attachment disc but no sharply-marked basilar muscles.

The other genera enumerated really concern us more here, as they are nearer to the forms whose evolution we are trying to elucidate. They have in common a more or less vermiform shape; in the broadest of them length predominates over breadth quite distinctly (even *Peachia* may be very long and narrow when alive), and in the narrowest their length is very many times their diameter. They typically have their base developed as a physa. The number of mesenteries is comparatively small, and most often either all are macrocnemes or else there is a distinction into macro- and microcnemes, although in some forms one would have to speak of a grading between larger and smaller mesenteries. The macrocnemes bear strong retractors which are generally more or less circumscribed and frequently reniform in outline in section. Among these forms *cinclides* occur fairly often. There is among them a complete absence of those characteristics which I have mentioned as typical of certain advanced forms—there are no well-marked sphincters, no large number of mesenteries grading off into each other, no sterility of the primary mesenteries taken as a whole, no well-marked foot-discs with basilar muscles, no very thick body-walls with tubercles and crests and tentacular swellings like those of *Actinauge*, etc., and no complete sinking of tentacular musculature into the mesogloea. Instances might be multiplied, but the general tendencies of evolution which I have indicated above are quite widely borne out by the generic series included in the nine families which I have outlined above. There are, needless to say, a good many exceptions here as everywhere else in the animal kingdom, but they hardly invalidate the main scheme. Further notes on these exceptions will be found on p. 508.

Before leaving this section of the subject, a brief study of

the evolution of retractor muscles and of definite pedal discs with basilar muscles, in correlation with one another and with the life of the animal, offers attractions. I am indebted to Prof. G. C. Bourne for a number of detailed suggestions connected with this problem. I have mentioned above that the anemones cited as being more or less primitive have all, except in the *Gonactinia*-group, strong retractors which are usually more or less circumscribed (see Text-fig. 11). They also have typically rounded aboral ends, and their general habit is to live more or less buried in sand or mud, or in tube-like holes. The forms among them with which I am personally acquainted, or of the habits of which I have knowledge from other sources, have the power of contracting with great violence and rapidity. An *Edwardsia* or a *Halcampa* can disappear below the sand in the twinkling of an eye. The powerful retractors come in here as shorteners of the long body in cases of emergency. Here we have an interesting case of adaption to a burrowing life or a life in holes. In the *Phellias* (which have the strong circumscribed retractors) described by Bourne and Haddon and others it is possible to trace a transition from burrowing forms with a real physa to forms with an adherent but physa-like base which anchor on to pebbles, shingle, etc. In such cases the action of the powerful retractors cups the physa-like adherent base and makes a sucker of it. This shows the first step towards the development of a true adherent base. From this point onwards there is no difficulty about imagining the evolution of a more definite and permanent pedal disc, and in correlation with it a change in the form of the lower ends of the mesenteries for insertion into it, and a differentiation of definite basilar and parieto-basilar muscles. But given this broad adherent base, a stronger body-wall, and a well-developed sphincter, the animal does not need to contract so violently. It has presumably left its sandy quarters and is attached to a rock or some other similar substratum, and one might expect its retractors to degenerate and become diffuse. This is further borne out if we remember that at the same time as

this evolution is progressing the mesenteries are increasing in number, and that therefore as soon as more of them have attained retractors, there will be less need for specially strong individual muscles on the primaries. On these grounds I think it is a fair conclusion that the general tendency is for circumscribed retractors to become diffused as evolution progresses. There are a few forms which retain the circumscribed retractor even though they have largely lost their other primitive characters. In these cases the life and habitat of the animal may be looked to for an explanation. A further note about them will be found on p. 511.

One fact cannot be passed over. It is not invariable for primitive forms to have powerful or circumscribed retractors; in *Gonactinia* and *Protanthea* the retractors are very feeble—hardly differentiated. In the first place I think it is probable that the ancestor of the *Actiniaria* as a whole would have weak retractors and a non-concentrated muscular system generally. It would no doubt possess longitudinal musculature in the ectoderm of the body-wall, which would obviate the need for strong retractors. It would probably be a small, delicate animal whose tissues would not offer much resistance to the forces of contraction. As far as the ectodermal muscle-sheet is concerned it might be compared with *Cerianthus*, especially as some authors consider a *Cerianthus*-like form to be primitive. *Cerianthus* inhabits sand and mud, and has practically no mesenterial musculature, but in substitution a very powerful ectodermal musculature in the body-wall. As Carlgren holds, this feature may be in part retained by *Protanthea* and *Gonactinia*, but it is lost in the higher anemones on the whole, with the exception of a number of unrelated forms which retain traces of it. It is not impossible that mode of life will help to account for this retention (or re-development)—in part at any rate. In *Aiptasia couchi*, for instance, the weakness of the rest of the musculature stands in need of a little aid from ectodermal muscle. The life conditions of *Gonactinia* and *Protanthea*

do not seem to indicate any special need for strong retractors. Both are small and delicate; they live in fairly shallow water attached to seaweed and other things. Carlgren records *Protanthea* on *Chætopterus*-tubes and *Gonactinia* on Ascidians and dead mussel shells. *Gonactinia* can creep by means of its tentacles, but can swim mouth foremost and so remove itself from any small disturbance. *Oractis*, which is probably related, is a small deep-water form. It is therefore possible to regard the *Protanthea* group as representatives of the most primitive condition retained by any existing forms, and to suppose that the rather more advanced forms with circumscribed retractors have developed these in correlation with mud-burrowing and life in cavities, and perhaps also in correlation with the loss of the ectodermal musculature of the body-wall. If this be the case we must look upon the circumscribed retractors as specialisations in otherwise primitive forms. The further development of lines of evolution starting from these forms, and involving a change to a fixed life and including increase in the number of mesenteries, would mean the loss of these special retractors in most cases and the differentiation of a larger number of diffuse ones.

With the above preface I will indicate as briefly as I can the line of evolution which seems most in accordance with the facts, as regards my nine families. Afterwards possible alternatives will be mentioned.

Following the lines indicated above, it is natural to choose as a starting-point that form which most nearly expresses the characters which have been enumerated as primitive. The group of the nine that comes nearest to this is the *Diadumenidæ*. The only difficulty here—and I do not personally consider it to be a difficulty—is that acontia are present. But, as has been noted before, acontia are only a variety of mesenterial filament, and if filaments have been acquired by the very simplest anemones, such as *Gonactinia*, why should it not be supposed that the slight differentiation needed to produce acontia appeared at a fairly early stage in the history of the group? If a form has gone far enough to acquire a meso-

gloœal sphincter, it has surely gone far enough to acquire acontia, and there is no valid reason why a start should not be made with a form possessing the latter. *Mena chilkaea*¹ fulfills our requirements almost exactly. It is rather small and delicate. The column is capable of considerable elongation, and has a small unmuscular basal disc never strongly adhesive, and capable of assuming a physa-like appearance. The delicate wall is pierced by cinclides. There is a weak mesoglœal sphincter. There are six pairs of macrocnemes with circumscribed retractors, and very few (usually 12) microcnemes, which are almost vestigial. Acontia are present. I think we may assume that this comes very near to the ancestral form we are looking for. It is a species, certainly, the simplicity of which may be due to retrogression, in correlation with its life (see p. 509) in brackish water, but that does not interfere with its giving the necessary clue to the primitive type. It is probably secondarily primitive.

My hypothetical ancestor may therefore be defined as follows:

Body-wall delicate and pierced by cinclides; form more or less elongate; six pairs of fertile macrocnemes with circumscribed retractors and with filaments; microcnemes absent or very few and quite rudimentary; acontia present; sphincter weak, mesoglœal, only just distinctly developed; base a physa.

It should be understood that this form, which I will call for convenience *Eosagartia*, is only suggested as the probable ancestor of the genera contained in the nine families above enumerated—the genera with mesoglœal sphincters or acontia, or both. It is by no means the ancestor of either the whole of the Actiniina or Actiniaria; it is about on a level with *Halcampa*, and very likely it shares with *Halcampa* a rather earlier common ancestor.

In order to make what follows clearer, I propose to give the hypothetical history of the group in narrative form, but of course I have no intention of stating that it *did* happen so, but am merely using that mode of expression as the clearest.

¹ *Mena* = n. nom. for *Phytocoetes*, pro parte. See p. 522.

Eosagartia lived in the sand, into which it could withdraw very suddenly when necessary by means of its powerful retractor muscles. In correlation with this kind of life it had a long body and a rounded base. The pores in its delicate body-wall helped to allow water to escape from inside it without bursting the wall, when it had to contract quickly. Its acontia were sometimes forced out through these pores by the strong jets of water which spurted out of them.

Some of the descendants of *Eosagartia* developed certain features which made them unlike their original parents. They acquired a basal disc, by which they attached themselves to solid objects, and the number of their microcnemes increased, and some of them began to assume in some degree the importance of macrocnemes. How far this particular branch of descendants diverged from their ancestral condition we do not know, but in the end they took to living in brackish water in India, very often returning to a life buried in mud (Pl. 22, fig. 13,; Text-fig. 28). This kind of life involved loss of some of their specialisations, and they became somewhat simplified again, so that in the end some of them almost went back to the condition of *Eosagartia*. Most of them even lost their mesogloal sphincter. The survivors of this branch, therefore, retain their primitive features in the main to this day. They are the *Diadumenidae*.

Another group of those descendants of *Eosagartia*, in which the microcnemes had begun to increase in number, began to develop a protective cuticle on the main part of their body. This meant that the wall lost delicacy, and was no longer a suitable place for pores, and these were lost also. About this time some of them began to attach themselves temporarily to bits of shingle by making a sucker out of their base—they pulled it inwards with their strong retractors. This led in some cases to the development of a more or less definite pedal disc. Another thing that happened was that in some of them the acontia began to degenerate, and in the forms now surviving it is possible to find, in this group, forms provided with good acontia and forms in which they are

rudimentary. Then, again, the microcnemes tended to grow filaments and acontia. But although many forms which followed this line of evolution still survive, they have never lost their six pairs of great macrocnemes bearing gonads and strong retractors as well as filaments, and reaching the actinopharynx, and the microcnemes are still more or less insignificant, and clearly marked off from the others. They have retained, too, as a rule, rather long bodies, and the power of introverting the disc and tentacles and the delicate neck or *capitulum* which bears them within the tougher cuticled *scapus* or middle part of the body. Even part of the *scapus* can be pulled in as well. Many of them have developed a better sphincter than *Eosagartia* had, and it has often divided into two parts—one in the *scapus* and one in the *capitulum*. This group of forms constitutes the *Phelliidae*.

Thirdly, some of the species related to the *Phelliidae* went a step further. They had already lost their cinclides. They did not lose the primitive distinction of the mesenteries into macrocnemes and microcnemes, but their acontia, from being rudimentary, disappeared entirely. They developed a rather more definite kind of adherent base. As regards the body-wall, they retained the division into a main *scapus* with cuticle, or with some sort of incrustation, and a submarginal non-cuticled *capitulum*. They survive in this condition as the *Marsupiferidae*. One of them has developed curious brood-pouches in the female.

It is now necessary to go back to the beginning and follow the further evolution, in quite another direction, of some others of those descendants of *Eosagartia* in which the number of microcnemes had begun to increase. These, instead of losing the delicacy of the wall, the pores, and the acontia, developed more as regards the mesenteries and the base. They adopted an adherent life, and this was followed by the development of a well-marked base. The microcnemes increased in importance, and in the end they developed so many structures that they approached the condition of the macrocnemes, and finally the distinction between the two kinds was lost. The

secondary mesenteries mostly acquired filaments and retractors, and often the work of producing gonads fell upon them, because the primaries had passed the climax of their growth rather early on. Although these things occurred, the primary mesenteries, which had originally been the macrocnemes, still remained predominant in one respect—they alone joined the actinopharynx, the others remaining imperfect. Here, then, a stage is reached where the distinction into macrocnemes and microcnemes is lost, and the mesenteries are arranged in graded cycles, but still only six pairs of mesenteries—the primaries—are perfect. As the muscular mesenteries increased in number and the body-wall often became rather less flimsy, and as the basal disc became better developed and the sphincter stronger, there was less need for the retractors of the primary mesenteries (the old macrocnemes) to be exceptionally powerful, and they degenerated in most cases, and became diffuse like those of the secondary or imperfect mesenteries (the original microcnemes). From this point onwards some forms began to diverge in one direction, some in another, but a number of forms got no further, and represent this stage at the present day as the *Metridiidae*.

There are one or two of the *Metridiidae* which either took to some kind of life which meant retrogression, or else did not quite keep up with the others in all respects; and these, though they have the typical mesentery character, have the mesogloœal sphincter either very weak and rudimentary or quite absent. Some of them have even kept or returned to the flimsy body-wall with a certain amount of muscle in its ectoderm, and a poorly developed base, which sometimes lets go its hold on the rock sand and, as the animal lies loosely on its side, is inflated so that it is half like a physa. This applies to *Aiptasia couchi*, for instance.

From this point onwards there are two distinct branches of further divergence to follow. Some of the forms near the present-day Metridians went in one direction, some in another.

Let us first follow those in which, to the very end, the six pairs of primary mesenteries so far predominated over the

others that they alone were perfect,¹ although the other mesenteries ran them close and bore filaments and retractors (except for the very young ones) and generally gonads as well. As regards other things, however, many forms began to follow a line similar to the one already traced in the Phelliidæ. The body-wall became generally tougher and thicker and lost its cinclides, while the lower part of it in many cases developed a cuticle, so that the body was in some degree divided into scapus and capitulum. But things went further than this, because some forms retired into deep or fairly deep water, possibly for refuge, their metabolism became slower, and they often developed not only a thick cartilaginous body-wall, but also used up spare energy by ornamenting it with knobs and crests, the crests sometimes breaking up into more knobs. In some cases the tentacles even developed great solid swellings or horns at their bases. The sphincter still remained strong, but the acontia began to degenerate, and among these forms, as among the Phelliidæ, forms may be found in which they are still well developed and others in which they are quite rudimentary. The genera which have evolved no further than so far indicated are the *Chondractiniidæ*.

Certain animals related to the earlier Chondractiniids not only lost their cinclides, but also all trace of acontia. They retired to deep water and their bodywall in some cases became remarkably ponderous—so thick that one would think the animal could hardly move (see Text-fig. 31). In these cases the sphincter degenerated and became less powerful, and sometimes even the tentacles were reduced, and they developed swellings of mesoglœa also. Some other animals related to the early Chondractiniids also lost their acontia as well as their cinclides, but, probably in correlation with life on shore, sometimes in deep cracks, they retained part of the primitive delicacy of tissues and some other primitive traits (see p. 511). But it is convenient to include them with the deep-water

¹ Except in a few cases where a very few other mesenteries attain perfection.

forms in one family, as the two sets have much in common. This family is the *Actinoscyphiidae*.

In order to understand the last part of this evolutionary history, it is necessary to make a start once more from the stage represented by the Metridiidae, and to follow the development of those forms which descended from that stage, but did not go in exactly the same direction as the Chondractiniids and Actinoscyphids.

From a form near *Aiptasia*, in which, although the distinction between macrocnemes and microcnemes had been lost, the primaries still retained their fertility (others sharing it), a number of forms went a step further. The primary mesenteries lost even such predominance as was given them by the fact that they alone were perfect, and the first cycle of secondary mesenteries, and even the second cycle of secondaries (i.e. the tertiaries, counting the cycles another way), became perfect also. At first the acontia, the cinclides and the fertility of the primary mesenteries were retained, and the present-day forms representing this phase of evolution are the true *Sagartiidae* in the strict sense, i.e. the genera *Sagartia*, *Cereus*, and *Artemidactis*. They have the mesogloœal sphincter well developed.

Some relatives of the *Sagartiidae* then began to follow a path similar in some respects to those already outlined as having been trodden by the Phelliidae and Marsupiferidae on the one hand, and the Chondractiniidae and Actinoscyphiidae on the other. Some forms retained, others lost the primitive fertility of the primary mesenteries. But the body-wall sometimes became thickened, and in all the cinclides were lost. There is only one described genus which definitely represents this particular stage, and that is *Choriactis*. It has many perfect mesenteries and thick body-wall without cinclides, but acontia are still present and the mesogloœal sphincter is well-developed. This is the type-genus of the family *Choriactidae*.

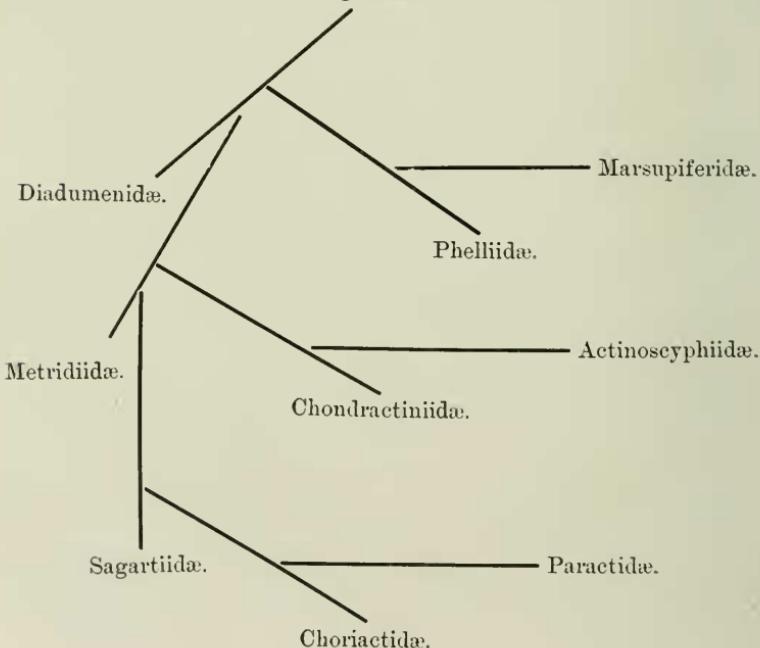
The final step is that by which the forms with numerous perfect mesenteries, and with no trace of distinction of

the mesenteries into macrocnemes and microcnemes, lost their acontia as well as their cinclides. In the majority of them the longitudinal musculature of the tentacles and radial musculature of the oral disc, which were primitively ectodermal, sank entirely into the mesogloea, and sometimes even became rather reduced. The forms representing this final stage are the *Paractidæ* in the strict sense, as defined on p. 548. Some of the genera still retain one or two primitive features, but apart from the other advanced tendencies, a number of them exhibit thick body-walls which may develop knobs or crests, and the tentacles may show basal swellings of mesogloea similar to those mentioned in connection with other families. In the Paractids the mesogloal sphincter is well developed.

The above statement gives in general outline an evolutionary history which seems to offer a reasonable explanation of the varied structure exhibited by the group.

It might be graphically represented in some such way as this :

Eosagartia.



The figure shows that the line of evolution from *Eosargartia* to the *Paractidae* is a fairly continuous one, affecting mesenteries first, and in the end involving loss of first cinclides and then acontia, the former in correlation chiefly with a change in the body-wall. Branching off from this main line are two others, running *parallel* with the later part of the first line, and both similarly involving loss of cinclides and finally of acontia. This evolutionary hypothesis explains the continuous evolution of the mesenteries, starting from a primitive condition with a small number of microcnemes. It assumes, of course, the loss of first cinclides and then acontia by three different series of forms independently; but I submit that it is easier to understand their disappearance in three different cases than it would be to understand their independent acquisition by three different sets of animals, which latter would have to be assumed if we started from some other point. The loss of such pores as cinclides is liable to happen to any number of animals progressing on the whole towards less delicacy of body-wall. I do not know whether one could find a reason why useful structures like acontia should disappear, but at all events there is no definite reason why they should not. It is possible that they were an experiment which did not prove so great an advantage as it might have done, and was dropped. Loss of activity and slower metabolism may help to account for the degeneration of such organs in deep-water forms (cf. reduction of gill-respiration in *Pleurotomaria*), and if these forms had not a sufficiently contractile body how could they expel the acontia? They are forced out, as far as we know, by currents of water escaping from the contracting body. In the case of shore forms and others to which this would not apply the former idea would have to be resorted to. I do not wish to push it too far or to over-emphasise it, but the disappearance of acontia does not seem to me to be a great difficulty, and there may be unknown causes that could lead to it.

It would be advisable now to consider whether there are any alternative ways of deriving these nine families from

ancestral forms, and how far any such are valuable. Opinions will naturally differ. The possibility of starting at the Paractidæ and working towards the other groups hardly needs examining, for surely no one would take a form with all the specialisations of *Catadiomene* (for instance) as primitive (see p. 488). Again, to start from *Actinoscyphia* or *Marsupifer* would be to work from forms with either thick walls and bulbous tentacles or with cuticle, and definite or well-developed pedal discs with basilar muscles, towards more delicate creatures with weaker base. It would assume independent acquisition in three cases of first acontia and then cinclides, although, as I have shown above, the presence of cinclides is not dependent on that of acontia. Such a scheme would end up near *Halcampa*, and is, I take it, out of the question.

The only reasonable alternative seems to be to start with *Eosagartia* as before, but to arrive at the Paractids eventually in a different way. To do this one might take the main line (involving loss of cinclides and then acontia in this case) through forms related to *Diadumenidæ*—*Phelliidæ*—*Marsupiferidæ*—*Actinoscyphiidæ*—*Paractidæ*, and assume on three independent lines the changes from a condition with a few to the eventual state where many mesenteries are perfect and there is no longer any distinction between macro- and microcnemes. The two secondary lines expressing this mesentery evolution would be parallel to each other and to the later part of the main line, and would be, respectively, the lines passing through relatives of—

- (a) *Diadumenidæ*—*Metridiidæ*—*Sagartiidæ*, and
- (b) *Phelliidæ*—*Chondractiniidæ*—*Choriactidæ*.

That the whole series of changes from the macrocneme condition to the state with numerous perfect mesenteries and no distinction into macrocnemes and microcnemes should take place on three independent lines, seems to me much less likely than that cinclides and acontia should be lost on three independent lines. It would be by no means impossible, and even seems to have taken place in some of the other *Actiniaria*

not under immediate discussion, but it would be the less safe of the two assumptions in this case. Again, if this suggested alternative scheme were adopted, it would not work out by means of so neat a series of graduated changes.

After studying the question, therefore, from many points of view and for a considerable time, I have not accepted any of the alternative possibilities, but have concluded that the scheme described in detail above is the most natural and probable. But even if the explanation is not accepted, the classification of the group into nine clearly-defined families will remain unaffected. Of course, if it should be considered that the nine families evolved separately from different ancestors a different explanation would have to be found. But that seems highly improbable, and since the various forms grow very easily out of one another (or rather out of one another's once-existent relatives), running back to an early *Halcampa*-like form with acontia, there seems no reason why in this case the mesogloœal sphincter should not denote common origin.

Before leaving the question of evolution, I should like to indicate the position in my scheme of *Flosmaris* (see pp. 441 and 484) and of any new anemones which may be discovered, representing other combinations than those here dealt with (see p. 485).

It is quite possible that *Flosmaris* might be evolved in either of two ways: it might be derived direct from a *Phellia*-like ancestor by increase in the number of macrocnemes, or it might be derived, as I suppose others to have been, from an *Eosagartia*-like form via an ancestor, hitherto unrecorded, in which the number of macrocnemes had increased instead of remaining six pairs only, but which had retained cinctiles as well as acontia. The loss of the cinctiles and development of a different body-wall would lead thence to *Flosmaris*. I do not wish at present to definitely prefer one of these alternatives until other forms are known. The first one seems the more obvious, but I think the other one is equally tenable, and if the intermediate ancestor mentioned were discovered—

it would represent one of the possible combinations—it might prove preferable. Although *Flosmaris* is externally like *Phellia* by possessing a scapus and capitulum, I do not think this necessarily means that *Phellia* is its ancestor; parallel developments are sometimes striking in anemones, and other forms have scapus and capitulum which could not be connected with *Phellia*.

I will not make any definite suggestions with regard to the evolution of the other possible combinations referred to on p. 485, which may come to hand, until they do so; but I may say that I have worked out the evolutionary scheme and the tree on p. 504 in such a way that new forms can be filled in without much difficulty.

VIII. NOTES ON EXCEPTIONAL GENERA.

There are a few genera presenting characteristics which make them exceptional in one or more respects from the general tendencies of the group as outlined in the foregoing evolutionary history. The existence of exceptions in no way disproves the general rule. In dealing with living forms it is impossible to divide everything up into absolutely water-tight compartments on a mechanical basis. The exceptions cited may be understood as either forms in which retrogression has taken place in correlation with mode of life, or in other cases as forms which have retained one or two primitive characteristics whilst losing others.

(1) Forms with no Sphincter.

The genera possessing acontia but no mesoglæal sphincter are *Diadumene*, *Phytocætes*, *Pelocætes*, *Halcampactis*, *Bartholomea* and *Aiptasiomorpha*. It will be noticed that all these forms occur in the three families which, according to my interpretation, are the most primitive of those here dealt with—i.e. the *Diadumenidæ*, *Metridiidæ* and *Phelliidæ*. After this the mesoglæal sphincter becomes fixed.

Diadumene, *Phytocætes*, and *Pelocætes* (Pl. 22, figs.

12, 13, Text-fig. 28).—These three forms live together with *Mena* in brackish water in India. A study of the excellent account of them given by Annandale (4, 5) will remove all doubt as to their being related to each other and derived from a common ancestor. *Mena* has the mesogloœal sphincter weakly developed; the other three agree in all other fundamental respects with it, and could on no account be separated from it, except of course generically, the generic differences being very marked. They may never have acquired the sphincter, but I think perhaps it is more likely that they have lost it. Except *Diadumene*, they are burrowing and sponge- and alga-inhabiting forms with long bodies, and the retention by all of them, even *Diadumene*, of strong retractors usually circumscribed does away with the need for a strong sphincter. The adaptation to life in brackish water, with a return very often to burrowing, might easily account for a retrogression or secondary simplification involving loss of the sphincter, or a checking of its development (it is hardly efficient even where present) and a general return to a fairly primitive condition.

Halcampactis.—This again is a form with strong retractors which may have lost or never acquired the sphincter. We are not even perfectly certain that it does not possess a very weak one. Farquhar states that it has no "well-defined" circular muscle, but, as Bourne has suggested (10, p. 67), a very small one may be present. In any case it agrees with some of the *Phelliidæ* in all other important respects, and one cannot doubt, on the evidence of the sum of the characters, that it is related to them. It is nearer *Phellia* than *Halcampa*, because it has acontia and no cinclides, whereas *Halcampa* has cinclides and no acontia.

Aiptasiomorpha and *Bartholomea*.—A number of species have been described under the names *Aiptasia* and *Aiptasioides*, on the assumption that the type-species of *Aiptasia* (*A. couuchi*) was devoid of a sphincter. The discovery of a weak mesogloœal sphincter (see p. 438) in *A. couuchi*, necessitates a certain readjustment of names, which will be

dealt with later on (p. 531). As a result there are now four genera—*Aiptasia* and *Heteractis*, in which a weak mesogloëal sphincter is present, and *Aiptasiomorpha* and *Bartholomea*, in which it is absent. The former genera contain *couchi*, *prima* and *pallida*, the latter *tagetes*, *annulata* and others. I take it that no one would suggest that *couchi*, *prima*, etc., are not closely related to *tagetes*, etc.; in all important features save the sphincter the two sets resemble one another. The mesogloëal sphincter is very weak in those which have it, but they provide a link between those without it and those in which it is strong. It looks as if *tagetes*, etc., had lost a muscle which was getting weak in *couchi*, etc. (or else as if the sphincter-development had been retarded while other organs evolved). The lax habit of *A. couchi* and its long non-retractile tentacles must be connected in some way with its mode of life, and would naturally be conducive to degeneration of the musculature. If *A. mutabilis* has, indeed, as stated by Simon, a diffuse endodermal sphincter, it must have been secondarily acquired to replace the lost mesogloëal one in connection with some new need for additional musculature (see, however, p. 467).

In consideration of the details collected here, it may be fairly claimed that all the forms enumerated as possessing acontia but no mesogloëal sphincter are quite clearly related to other acontiated forms, but have lost the sphincter (or more improbably never acquired it) in correlation with mode of life or something similar. I venture to suggest even that it is not impossible that in some of these forms, at any rate, there is in fact a very weak mesogloëal sphincter. Very feeble sphincters are easily overlooked and require good material for their detection.

(2) Forms Retaining Certain Primitive Characters.

I do not suggest that enough is known about the habits of the animals that will be mentioned to fully account for the structural correlations which make them exceptional to the general tendencies outlined in my evolutionary scheme. But

a detailed study of their life and conditions might well reveal an adequate reason in each case.

Paraphellia and *Isoparactis* (Text-figs. 29, 30) have retained circumscribed retractors on the primary mesenteries (not on the others)—a characteristic which their relatives have lost. *Paraphellia* generally lives on a sandy bottom, and it may need the powerful retractors to help the sphincter to withdraw the tentacular crown very suddenly to avoid its being bitten off by hunting fish in search of such things as molluses emerging foot-foremost from the sand. This or some similar reason would account for retention or re-development of the circumscribed muscles. *Isoparactis* lives under stones and in dark places. Another anemone which has to some extent retained circumscription of retractors is *Hormosoma*, an Antarctic form, the life conditions of which I do not know. The retractors in this case are less powerful and definitely circumscribed than in the other two.

Stomphia, *Isoparactis*, *Paranthus*, etc.—The tendency towards the formation of a thick or cartilaginous or encased body-wall is not universal though general, and sometimes a thin or comparatively thin one persists. *Stomphia* and *Isoparactis*, whilst possessing a firm and well-developed mesogloea, vary from moderately thick to quite thin walls. *Paranthus* is another case in point. *Paranthus* and *Isoparactis* are shore forms; *Stomphia* lives in moderate depths. It is natural, of course, to expect thickening of the wall to be best developed in deep-water forms, which is actually the case, but even here *Ophiodiscus* is not really thick-walled. The exact thickness varies of course according to how much the body is distended with water, but probably the thickest walls cannot be much altered.

Gonads.—Although the general tendency seems to be towards sterility of the primary mesenteries, a number of forms still produce gonads on the primaries as well as some of the others right to the end of the series. These forms are some *Aiptasids*, *Isoparactis*, *Paranthus* in some cases, the true *Sagartiidae* (*Sagartia*, *Cereus* and *Artemi-*

dactis), and some of the Paractid genera. The Aiptasids and Sagartids are still not so far removed as many forms from the original state of the group, and we can understand the retention in such cases. I can offer no explanation of it in the Paractid case. Isoparactis and Paranthus are curious forms, exceptional in most things. Further reference will be made to them in enumerating the genera.

IX. DISCUSSION OF GENERIC CHARACTERS.

(1) Form of Base.—When a pedal disc is present it may vary considerably in one and the same species, as regards its form, according to environment, and is therefore not valuable for a specific or generic character unless in any given case it exhibits certain characteristics invariably. Verrill states quite clearly, for instance (93), that in *Actinostola callosa*, *Hormathia longicornis* and *H. nodosa* the base takes the form of a hollow mud-clasping cup when the animal is living in a muddy situation, but that when it is living on a hard, stony bottom the base takes the form of a flat attachment-surface. In the genus *Actinoscyphia* the base may form a mud-cup, or it may be adherent or clasp the spine of some animal and so become long and slit-like. In *Actinauge richardi* stages are found from a broad, flat adhesive disc to a deep cup-like hollow with only a small circular opening, according to habitat. It is probable also that anemones which live habitually on such supports as Gorgonians and have one axis longer than the other would be normal in shape if they grew up under more ordinary conditions, and this one feature is not enough to differentiate them generically from ordinary forms if they agree in all the more important respects.

(2) Body-wall.—Presence or absence of definite verrucæ or acrorhagi and similar structures are obviously useful generic characters. Presence or absence of a cuticle on the scapus may also be valuable. With regard to the presence or absence of "capitular ridges" in some forms, it would seem wise to

discard the use of this character as a generic one. In *Hormathia digitata* the capitulum may be smooth (Haddon's specimens) or definitely ridged (many of Carlgren's specimens). In two specimens of this species which I have examined one had the ridges much better developed than the other. I have already shown (80) how much these ridges vary in *Actinauge richardi*, in which they may be nearly absent or very prominent. When present they are more or less regularly arranged in some *Hormathias*, but in *Chondrodactis duplicata* have no definite arrangement, and their presence in this latter case cannot separate *C. duplicata* from other species of *Chondrodactis* without definite ridges, because in other ways the relationship is so clear. In *Cymbactis gossei* there are "capitular ridges" which are quite prominent but without regularity; in this case the only recorded specimen was strongly contracted, with the upper part of the body introverted, and the ridges seemed to me to be due to the contraction of the thick wall, and would probably disappear on expansion. The species seems to be clearly a *Cymbactis* in spite of them. Considering the general variability of these ridges, even within one and the same species, it would seem best to discard this somewhat trivial character as a sole mark of difference between two genera.

The actual thickness of the body-wall itself is another debatable point. It has seemed a rather useful character sometimes and has actually been used. But recently I have come across cases in which it is difficult to decide whether such-and-such a species should be classed as "thick-walled" or "thin-walled." For instance, some specimens I have of *Stomphia churchiae* have a quite moderately tough and thick wall for the size of the animal, but I would not call them exactly "thick-walled" or "thin-walled." Carlgren's figure of *Stomphia* (Taf. i, fig. 11, 1893) shows quite a thin-walled specimen, so it is evidently variable. Then when I was studying *S. churchiae* its whole organisation reminded me very strongly of a form I had previously described as

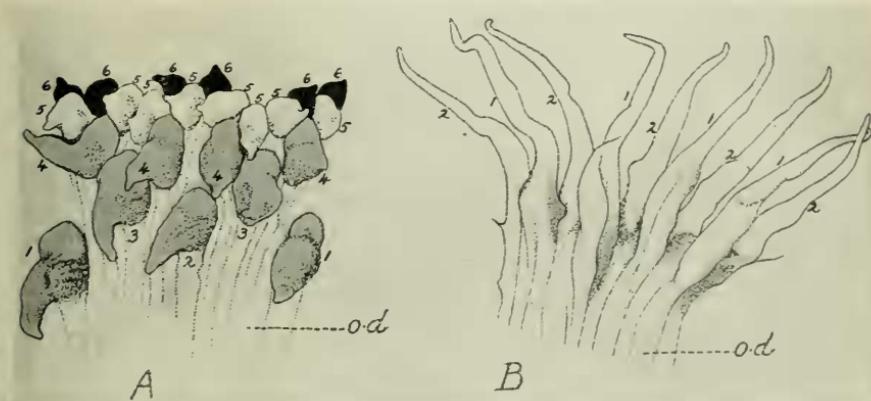
Cymbactis selaginella (79, p. 36), both as regards arrangement and appearance of tentacles and mesenteries and as regards detail, so that I have no hesitation in saying that both ought to be included in one genus. But *C. selaginella* may be called definitely "thick-walled," though not necessarily so, and evidently here the genus cannot be characterised one way or the other since it must also include *S. churchiae*. In *Chondrodactis*, again, one finds grades of thickness, from moderately thin in part in *C. pulchra* to very thick in some specimens of *C. duplicata*. In *Actinauge richardi* different shades are found. Some specimens have a very thick, firm mesogloea, quite remarkably solid for the size of the animal, while in others it varies in thickness, till in cases where the body has been distended with water the wall is so very thin that it is semi-transparent and the mesenterial insertions show through it. Since this character is liable to vary and one cannot draw a line between "thin-walled" and "thick-walled" forms, it would probably be the best to discard it also, in most cases, as a sole difference between one genus and another.

(3) Tentacles.—The shape of these organs when they are simple is hardly a useful character for defining genera, because it varies very greatly from time to time in one and the same living individual, and within the limits of one species. The form of the tentacles in a preserved specimen will depend chiefly on the circumstances of the animal's death. I have, for instance, two specimens of *Phytocœtes gangeticus* preserved in one tube; one of them has the tentacles contracted—short, and comparatively stout and stiff; in the other they are expanded, and are very long and slender and quite flabby.

One character has struck me during the course of my work as being a distinctly valid one for the separation of genera. In *Actinoscyphia*, *Chondrodactis* and *Polysiphonia*, for instance (three genera not closely related to one another)—genera containing large, sometimes very large, species—there are never more than two cycles of tentacles, although the

mesenteries are arranged in several cycles in the usual way. It may be urged that the exact number of cycles of tentacles is not much to go by, and in many cases it is not. But in the cases referred to there is a wide oral disc, and the tentacles are all placed in two alternating cycles at the very edge of it, as a rule all of them more or less communicating with the margin of the body by means of their basal swellings, the outer ones only being more definitely marginal than the

TEXT-FIG. 26.



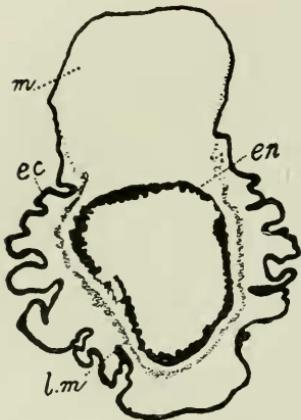
A. Portion of oral disc and tentacles of *Catadiomene atrostoma* (diagrammatic). B. Portion of oral disc and tentacles of *Actinoscyphia saginata* (diagrammatic). o.d. Oral disc. Numbers indicate tentacle-cycles.

inner. The appearance is quite different from the usual cycle-arrangement, and there is no marked diversity in size between the outer and inner tentacles. I have attempted to bring out this difference in Text-fig. 26. A represents part of the disc and tentacles of *Catadiomene atrostoma* (diagrammatic), showing the ordinary arrangement in several cycles—five and part of a sixth in this case. B shows part of disc and tentacles of *Actinoscyphia saginata* (diagrammatic), with the two alternating cycles only. In A the sixth cycle tentacles are black, the fifth cycle white, the

others grey. In anemones attaining so large a size as many of these, it is quite unusual for the tentacles to constitute only two marginal cycles, while the mesenteries at the same time arrange themselves in several cycles in the usual way. It probably indicates an unusual mode of appearance of the tentacles, and should form the basis of a clear generic character. Of course there will be a stage in the life of any young anemone when only two cycles of tentacles are present,

but I am speaking of adult forms, the majority of which attain several cycles.

TEXT-FIG. 27.



Transverse section of tentacle of *Catadiomene atrostoma*. *l.m.* Longitudinal musculature. *ec.* Ectoderm. *en.* Endoderm. *mv.* Mesogloea.

in other respects, and even when the swellings are present they may be variable in development, so that in one and the same species they may be very large and conspicuous in one individual, and so small as to be hard to detect at all in another. But they may be detected with care even at their weakest, and it is their *presence*, not their *size*, that constitutes the generic character.

Another interesting development is shown by the tentacles of certain relatives of *Aiptasia*—*Heteractis* and *Bartho-*

Iomea (see pp. 531-2). In these genera the tentacles develop curious thickenings, raised above the general surface of the tentacle, and which may take the form of spherical tubercles or of incomplete annuli or spiral bands. These are perfectly definite structures, differing histologically from the rest of the tentacle chiefly in that they are batteries of nematocysts; the ectodermal musculature of the tentacles may also be reduced in them. As far as I can glean from the accounts I have of these species, the presence of the bands on a portion of the tentacle (*B. peruviana*) or over a greater part of its extent is a constant character. It seems to be quite as worthy of generic rank as the presence of basal mesogloal swellings, and is a very convenient and easily made-out feature. The genera with and without these curious tentacles are certainly nearly related, but for distinguishing genera one does not need many differences. If it should be shown that the presence of the thickenings is variable and that they are absent in certain individuals that might alter the matter, but even then I am not sure that the potentiality for producing them in one species and the inability to do so in another would not be a sound generic distinction.

(4) Mesenteries.—The distribution of gonads on the mesenteries is of general use in a broad sense as indicating evolutionary tendencies within the whole group, and in some families either one method or another is adopted throughout. But some of the higher families are variable in this respect.

In the families Diadumenidae, Phelliidae and Marsupiferidae, where there is a division of the mesenteries into macrocnemes and microcnemes, the distribution of gonads of course follows and forms part of this distinction, the gonads being borne by the macrocnemes except in exceptional individuals.

In the families where there is no such division into macro- and microcnemes there are two in which one rule is universal. In the Chondractiniidae the primary mesenteries are sterile, and in the Sagartiidae (sens. strict.) most or all of them are fertile, as well as others. But in the remaining families

the rule is different for different genera. In most cases all the species in a genus adopt exclusively one condition or the other—i.e. either they all have sterile primaries, or they all have them fertile. But there are a few cases of variation even within one genus or species, and it does not seem wise to separate two species from each other on the sole ground that one has fertile and the other sterile primaries, although it is very useful to mention the facts of the case in a definition. Miss MacGuire (66) records two specimens of *Paranthus chromatodermis*, one of which had fertile and the other sterile primaries, some of the other mesenteries, in the second case, being fertile; in the first case some secondaries were fertile as well as the primaries. In *Bolocera*, a genus outside the immediate scope of this paper, some species have fertile and some sterile primaries, and in *B. longicornis* it seems as if different *individuals* might have fertile or sterile primaries. In any case, of course some of the non-primaries are fertile in these *Boloceras*.

(5) *Musculature*.—A good character for distinguishing genera from one another is the form of the retractor muscles of the mesenteries. Of course in some families they are all of one type, but in cases where they vary the distinction is a useful one. *Paraphellia* is easily distinguished from *Leptotrichia* and *Hormathia*, for instance, by having among other things circumscribed retractors on its primary mesenteries, while they have diffuse ones. *Isoparactis*, again, is clearly marked off from *Paranthus* by its circumscribed retractors. There are some genera, it is true, in which, although more or less diffuse retractors are the rule, there is a tendency towards circumscription in some species. This applies to *Sagartia* and *Aiptasiomorpha* and *Bartholomea*, and it is interesting to note that these are, according to the evolutionary idea developed above, survivors of some of the very forms in which the transition from circumscribed to diffuse retractors would be taking place, or would have been actually accomplished in most cases, *Aiptasiomorpha* being one survivor of the earliest forms to lose the macro-

cneme and microcneme distinction, and *Sagartia* one survivor of the first set of forms to attain numerous perfect mesenteries.

The character of the individual muscle-processes of the retractors is certainly not usually of generic value, though it appears to be capable of distinguishing species from one another in some cases.

It is a clear and simple distinction to place in separate genera forms which have the longitudinal tentacular musculature ectodermal and others which have it embedded in the mesogloea. This seems to be a natural and stable distinction. There are a few cases in which the musculature is mesoectodermal, and these must be judged according to the requirements of the individual case.

With regard to the sphincter, it avoids confusion and is a natural arrangement to place forms with no sphincter in different genera from those with a weak mesogloea! one. If the sphincter is endodermal, its diffuseness or circumscriptio often form simple generic features, but if it is mesogloea! its form seems to vary too much to be of use in classification.

(6) Summary.—It has been attempted to show that the exact form of the pedal disc, the presence or absence of capitular ridges, the thickness of the body-wall, and the form of the tentacles apart from actual structural differentiation of parts of them, are characters which it would be profitable to discard as sole generic distinctions; that the distribution of gonads is not invariably a reliable generic character; and that presence or absence of definite verrucæ and aerorhagi, and of a cuticle in some cases, the presence or absence of basal swellings or other tentacular specialisations, the limitation of the cycles of tentacles to two only (at the same time as the mesenteries are normally arranged in several cycles) in some forms, the form of the retractor muscles in most cases, the position of the longitudinal tentacular musculature (whether ectodermal and mesogloea!), and the presence or absence of the mesogloea! sphincter, are more valuable characters which may usually be emphasised in distinguishing genera. I have

shown before (79, p. 4) that the length of the body in proportion to its height may be a valueless character in certain cases, although some aspects of the form of the body are permissible characters for differentiation. This does not, of course, survey the field of generic characters at all completely, but it provides a basis for the re-defining of the genera especially dealt with in this paper. Individual cases have, of course, their own needs, which may except them from some fairly general principle. It should of course be understood that in suggesting that certain generic characters should be allowed to lapse, I am not intending omission of any mention of them, but merely that any one of them should not be made ground for separating two given species, otherwise similar, into different genera.

X. DEFINITIONS OF THE NEW AND REVISED FAMILIES AND OF THE GENERA CONTAINED IN THEM.

Family 1. DIADUMENIDÆ, n. fam.

METRIDIINÆ as used by Annandale, 1915, *pro parte*.

Actiniina. Pedal disc may be well developed or so reduced as practically to form a physa. Body-wall delicate, without cuticle, pierced by cinclides. Tentacles simple, their longitudinal musculature ectodermal. Oral disc simple or branched. Mesenteries divided into macrocnemes and microcnemes, but in one genus the division not sharply marked and may be practically lost in some individuals. Six pairs of macrocnemes which bear well-developed and usually circumscribed retractors and (with some exceptions in some individuals) gonads and filaments. A variable number of microcnemes which are more or less rudimentary according to genus; they are typically rudimentary, but in one species some of them may, exceptionally, bear gonad and filament, and in another some of them may attain considerable development; but even at the best some of them are rudimentary. Acontia present. Sphincter absent or weak mesogloœal, but relationship of forms without it to forms with it quite clear.

Genera: DIADUMENE, PELOCETES, PHYTOCETES, MENA.

DIADUMENE, n. nom. (see also p. 457).

METRIDIUM as used by Annandale (1907, p. 47, and 1915, p. 76) for M. SCHILLERIANUM.

NOT METRIDIUM, Oken.

Diadumenidae with broad, well-developed base. Column usually with vertically-arranged rows of suckers. Cinclides scattered. A convex ring-like collar present round upper part of column in expansion. Tentacles in several cycles. Oral disc simple, retractile. Microcnemes in 3-5 cycles; in some *individuals* gonads may be found on some of them; and although some are always rudimentary, some of them may bear filament and longitudinal muscle. No mesogloal sphincter. Retractors of macrocnemes may tend to be diffuse.

Species: D. schilleriana, Stoliczka (*Sagartia schilleriana*, Stoliczka, 1869, p. 28. See Annandale, 1907, p. 47, etc., and 1915, pp. 72-78). (See Pl. 22, fig. 12.)

The sole recorded species of the genus Diadumene was originally described by Stoliczka as *Sagartia schilleriana*. It has more recently been made the subject of research by Annandale (1907, 1915), who has worked out in great detail both its anatomy and its relationships with Pelocetes, Phytocetes and Mena. He has included it, however, in the genus Metridium, Oken, which, though a minor matter, can hardly be correct. If we compare Metridium, as typified by M. dianthus, with S. schilleriana we find the following differences.

M. DIANTHUS.

Column smooth.

Oral disc much lobed in adult.

Sphincter mesogloal, well developed.

Primary mesenteries sterile.

Radial musculature of oral disc sometimes partly mesogloal.

Mesenteries forming a graded series, not divided into macrocnemes and microcnemes, their retractors diffuse. Number of perfect mesenteries variable, although the six sterile primary pairs are often alone perfect. Imperfect mesenteries, many of them fertile.

S. SCHILLERIANA.

Column usually with suckers.

Oral disc simple in adult.

No mesogloal sphincter.

Primary mesenteries fertile.

Radial musculature of oral disc ectodermal.

Mesenteries here, although not fully divided into macrocnemes and microcnemes, tend that way, especially in some individuals where only the primaries are fertile. Only the macrocnemes perfect. Retractors more tending to circumscription than in M. dianthus.

These differences are not all of equal weight, but some of them are important, and taken together they show that the two forms are very different and cannot be included in the same genus. My case for allocating them to different families will be found in the earlier parts of the paper and really depends more upon the relatives of *schilleriana* than upon that species itself, since it is aberrant from the general tendencies of its group. A new name is therefore required for the genus containing *schilleriana*, which is no more a *Sagartia* than a *Metridium*, and I have proposed *Diadumene* for it. This name is also a convenient one to work into the name of the new family to which *Diadumene* and its relatives belong.

PELOCETES. Annandale, 1915, p. 85. (See Text-fig. 28 and Pl. 22, fig. 13.)

Diadumenidae with the basal disc much reduced, the aboral extremity capable of assuming a physa-like appearance and shape. Column vermiciform, with no collar, with suckers in the upper part arranged in vertical rows, and with cinclides also arranged in vertical rows in the upper part. The majority of the tentacles arranged in groups, each of which is placed on a flattened pedicel or outgrowth of the reduced, non-retractile oral disc. The only recorded species has thirty-six microcnemes, of which some are occasionally fertile, though as a rule they are rudimentary (Text-fig. 28). No mesogloal sphincter.

Species: *P. exul*, Annandale, 1907, p. 48, etc., and 1915, pp. 72-76, 86. (See Text-fig. 28 and Pl. 22, fig. 13.)

PHYTOCETES. Annandale, 1915, p. 78.

Diadumenidae with basal disc small and unmuscular, never strongly adhesive, the aboral extremity capable of assuming a physa-like shape and appearance. Column capable of considerable elongation but protean in form, smooth and very thin, the cinclides scattered in the upper part. Tentacles thread-like in full expansion, retractile. Oral disc simple. In the only recorded species there are usually twelve microcnemes, all of them almost vestigial. No mesogloal sphincter.

Species: *P. gangeticus*, Annandale, 1915, pp. 72-76, 79. (See also 1907.)

MENA, n. gen.

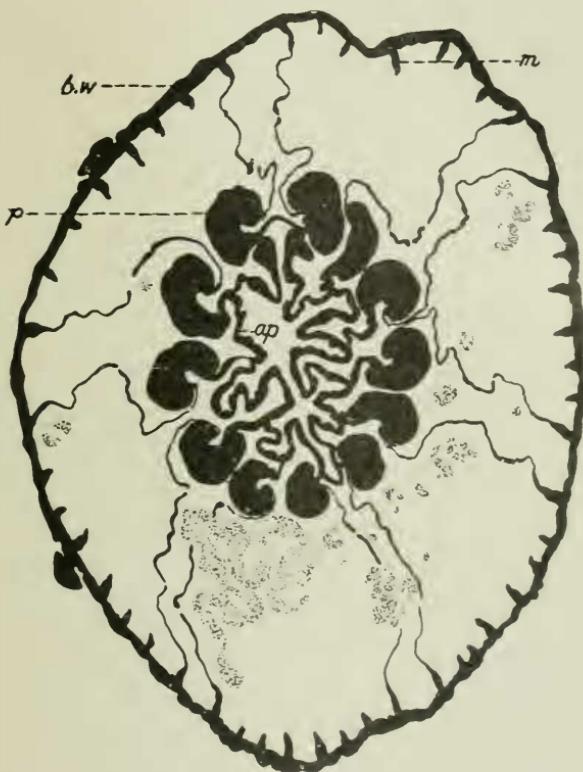
PHYTOCETES, Annandale, 1915, p. 78, pro parte.

Differs from *Phytocetes* by having a weak mesogloal sphincter, and, in the only recorded species, minute papillæ on the body-wall.

Species: *M. chilkaea*, Annandale, 1915, p. 82. (See also pp. 72-76.)

I have proposed a new genus (Mena) for the reception of Annandale's *Phytocetes chilkaeus*, because it avoids confusion in identifying to have forms with no sphincter

TEXT-FIG. 28.



Transverse section of body of *Pelocetes exul*. *ap.* Actinopharynx.
bw. Body-wall. *m.* Microcneme. *r.* Retractor.

separated from those with a mesogloal one; and the difference is one of enough importance to warrant separation. *Halocampa* is distinguished from *Haleampoides*, and *Aiptasia* from *Aiptasiomorpha*, in the same way.

Family 2. PHELLIIDÆ.

PHELLINÆ, Verrill, 1868, p. 324, 1869, p. 489.

PHELLINÆ as used by Haddon, 1898, p. 452.

NOT *PHELLINÆ* as used by Carlgren, 1893, p. 109, except for *PHELLIA* itself.

PHELLIIDÆ, Bourne, 1918, p. 84.

Actiniina. Body more or less definitely divided into a middle part or scapus provided with cuticle which is sometimes deciduous; scapus may be incrusted; a usually more delicate or extensile capitulum without cuticle, and which can be introverted; and a base which may be adherent or may resemble a physa. Cinclides absent. Tentacles and oral disc simple. Longitudinal musculature of tentacles usually ectodermal, sometimes meso-ectodermal. Radial peristomial musculature may be absent. Mesenteries divided into macrocnemes and microcnemes. Six pairs (or rarely fewer and rarely a very few more than six pairs) of macrocnemes which bear circumscribed retractors, filaments, and most or all of them gonads. A variable number of microcnemes which are more or less rudimentary; they bear no gonads, but some of them may bear acontia and filaments (usually very small ones) and vestiges of longitudinal musculature; their only well-developed muscles are the parietals. Acontia present, sometimes rudimentary. Sphincter usually mesoglœal, rarely absent, sometimes divided into a thicker scapar and thinner capitular portion.

Genera: *PHELLIA*, *DECAPHELLIA*, *HALCAMPACTIS*, and perhaps *ISOPHELLIA*.

Doubtful genera which may possibly find a place here are *Octophellia*, Andres, and *Ilyactis*, Andres.

PHELLIA, Gosse, Ann. N.H., 3, ii, 193, and 1860, p. 134.

Phelliidæ with base of variable development; it may be distinctly adherent, or may be more or less inflatable and comparable to a physa, and may be somewhat reduced. Peristomial musculature absent or reduced, causing the mouth to gape (always?). Six pairs of macrocnemes, usually all fertile. Microcnemes variable in number. Acontia variable, sometimes rudimentary. Sphincter mesoglœal, typically divided into a broader portion in the scapus and a narrower one in

the capitulum. Longitudinal musculature of the tentacles ectodermal, may be very powerful, or sometimes meso-ectodermal. Form of body variable; may be elongate.

Species: *P. murocineta*, Gosse, Ann. N.H., 3, ii, 193, and 1860, p. 135, is the type of the genus. Other species are numerous.

DECAPHELLIA, Bourne, 1918, p. 60.

Phelliidæ "with the characters of *Phellia*, but the capitulum has no musculature except for a mesogloal sphincter at its distal extremity, and there are only ten complete macromesenteries¹ bearing longitudinal retractor muscles."

Species: *D. psammomitra*, Bourne, 1918, p. 60.

HALCAMPACTIS, Farquhar, 1898, p. 530.

Phelliidæ with a rounded aboral extremity or physa. Six pairs of macrocnemes, and in the only anatomically described species six pairs of microcnemes. Body-wall provided with minute suckers; cuticle deciduous. No sharply-defined sphincter.

Species: *H. mirabilis*, Farquhar, 1898, p. 530. *H. dubia*, Stuckey, 1909, p. 387.

ISOPHELLIA, Carlgren, 1900, p. 72. (See p. 487.)

? Phelliidæ. Basal disc not sharply marked off. Scapus long, with numerous small papillæ to which sand-grains are attached. Capitulum smaller, without papillæ, smooth. Tentacles simple, in several cycles in the adult, their longitudinal musculature ectodermal. The most proximal part of the mesogloal sphincter sometimes separated from the remaining part. Macrocnemes of the first cycle as usual, six pairs, with gonads and strong retractors. Half the mesenteries (three couples) of the second cycle may also be macrocnemes like the primary mesenteries; the rest of the second cycle then imperfect and with weak or no distinct retractors. Third cycle consists of microcnemes. Probably more microcnemes present in distal part of body. Gonads found on those of the second-cycle mesenteries which are macrocnemes, and on at least one of the weaker second-cycle mesenteries.

Species: *I. sabulosa*, Carlgren, 1900, p. 72. (See p. 487.)

For a discussion of the systematic position of this genus see p. 487.

Family 3. MARSUPIFERIDÆ, n. fam.

PARACTIDÆ as used by Carlgren, 1901 and 1902, pro parte.

Actiniina. Pedal disc of variable extent. Column divided

¹ Macrocnemes.

into a cuticled or encrusted scapus and a naked capitulum. No cinclides. Tentacles simple, their longitudinal musculature ectodermal. Oral disc simple. Mesenteries divided into macrocnemes and microcnemes. Six pairs of macrocnemes with powerful retractors, gonads and filaments. The microcnemes may be broad, but are devoid of gonads, filaments and definite retractors. No acontia. Sphincter mesoglœal, double or single. Brood-pouches may develop in connection with the microcnemes of the female.

Genera: MARSUPIFER, PHELIOMORPHA.

It is not impossible that the doubtful genera *Phelliopsis*, Verrill, and *Cactosoma*, Dan., may find a place here.

MARSUPIFER, Carlgren, 1901.

Marsupiferidæ with definite base. Column smooth but for the cuticle of the scapus, capitulum naked and introvertible. Six pairs of macrocnemes, few microcnemes. Sphincter well developed, double. Female, in the only recorded species, with six brood-pouches developed in connection with the microcnemes.

Species: *M. valdiviae*, Carlgren, 1901.

PHELIOMORPHA, Carlgren, 1902.

PHELLIA as used by Danielssen, 1887, pro parte.

ISOPHELLIA, Carlgren, 1900, p. 52, pro parte.

Marsupiferidæ with base which may not be broad. Scapus with papillæ attaching sand-grains. Six pairs of macrocnemes and a few microcnemes. Sphincter very weak, single, lying just at the bases of the tentacles.

Species: *P. crassa*, Danielssen. (See Carlgren, 1902.)

Family 4. METRIDIIDÆ.

METRIDINÆ. Carlgren, 1893, p. 101.

Actiniina. Definite base, which may be broad or may be small and weakly adherent. Body-wall delicate or fairly firm, but with no cuticle; pierced by cinclides. Tentacles simple or with curious spherical or ring-like or spiral protuberances either near the tip or spread over the whole tentacle; but without aboreal basal thickenings of the mesoglœa. Longitudinal musculature of tentacles ectodermal or meso-ectodermal. Oral disc simple, undulate, or lobed. Mesenteries

not divided into macrocnemes and microcnemes. Number of perfect mesenteries typically six pairs only, but sometimes a few more perfect mesenteries are present in certain individuals of a species; or the typical number for a species may be eight pairs. Retractor muscles diffuse or with a tendency to circumscription. Perfect mesenteries fertile or sterile, usually the latter. *Acontia* present. *Sphincter mesoglœal*, strong or weak, sometimes absent; perhaps even weak endodermal in one case, those forms in which it is absent being clearly related to those which have it.

Genera: *METRIDIUM*, *CALLIACTIS*, *ADAMSIA*, *AIPTASIA*, *AIPTASIO-MORPHA*, *HETERACTIS*, *BARTHOLOMEA*.

Another genus which may possibly come here is *Stelidiactis*, Dan.

METRIDIUM, Oken, 1816.

ACTINOLOBA, Blainville, 1830.

Metridiidae with well-developed base. Body-wall smooth, with a very distinct circular collar round the upper part, in expansion: it is less evident in the young than in the adult. Cinclides scattered in the delicate wall below the region of the sphincter. Oral disc circular in the young, but deeply and conspicuously lobed in the adult, bearing many simple tentacles; its radial musculature may be ectodermal or partly mesoglœal, though the longitudinal musculature of the tentacles is ectodermal. Perfect mesenteries very variable in number and often irregular in development. In the majority of individuals the number of perfect pairs is between six and eleven, and of these individuals a considerable number have the standard six pairs alone perfect. More rarely there are fewer than six pairs perfect, and still less often are more than eleven pairs perfect. This irregularity is probably connected with the fact that asexual reproduction, especially by means of basal fragmentation, is of frequent occurrence. The six primary pairs of mesenteries are sterile. *Sphincter* well developed, mesoglœal, simple. Retractors diffuse, sometimes short and broad in section.

Species: The genotype is *M. dianthus*, Ellis, 1768, p. 428. (See also Carlgren, 1893, p. 102. Torrey, 1898 and 1902. McMurrich, 1901, etc.)

The above definition of *Metridium* may perhaps prove to be too narrow and exclusive, but for the present I have drawn it up chiefly with regard to the type-species *M. dianthus*, of which *M. marginatum* and *M. fimbriatum* are probably

synonyms (see McMurrich, 1901). Whether it will need modification when more is known of other species remains to be seen, but no forms in which the adult has a non-lobed disc or no collar should be included in it. Anyone who has seen *M. dianthus* alive and healthy cannot have failed to note these two striking characters. Even in the young one begins to see the collar and the plumpy character of the tentacles. If it should be found that there are other species like *Metridium* but in which the disc in the adult remains entire, a new genus will be required for them. It is possible that *M. parvulum*, McMurrich, 1904, and *M. canum*, Stuckey, 1913, are such forms, or, on the other hand, they may be young forms. For discussion of *M. schillerianum*, Stoliczka, which is not really a *Metridium*, see p. 521.

CALLIACTIS, Verrill, 1869, p. 481.

SAGARTIA as used by Gosse, 1860, pro parte. (S. PARASITICA.)

ADAMSIA as used by M. Edw., 1857, pro parte, by Andres, 1883, p. 366, pro parte.

Metridiidae with well-developed base. Column more or less cylindrical, not distorted; its wall may be firm or rather thick, and in some cases may form a kind of membranous investment, which is often shed, over part of the column. Cinclides in one or more horizontal rows near base of column; they may or may not be mounted on small tubercles. No collar. Margin tentaculate. Sometimes the oral and pedal discs are expanded beyond the column; the former is not lobed but may be somewhat undulate; its radial musculature may be partly mesogloal. Tentacles simple, in more than two cycles¹ in the adult, their longitudinal musculature ectodermal or meso-ectodermal. Six pairs of perfect mesenteries which are sterile. Retractors diffuse. The species usually live on a shell inhabited by a hermit crab, but not invariably. Sphincter mesogloal.

Species: Genotype, *C. decorata*, Drayton in Dana, 1849.

Others are *C. variegata*, Verrill, 1869, p. 481.

C. tricolor, Lesueur, 1817, p. 171 (= *C. bicolor*, Les., 1817, p. 171 = *C. egletes*, D. & M., 1866, p. 134. See also McMurrich, 1898.)

¹ It should be understood that when "tentacles in more than two cycles" appears in a definition, it does not exclude from the genus any species which may never attain more than two cycles because of extreme smallness when adult, and does not refer to young specimens.

C. fusca, Q. & G. (*fusco-rubra*, Q. & G., 1833, p. 145, *fusca*, M. Edw., 1857, p. 281).

C. polypus, Forskål, 1775, p. 102. (See Hertwig, 1882, p. 74, and Carlgren, 1900.)

C. miriam, H. & S., 1893, p. 130, Haddon, 1898, p. 457.

C. reticulata, Stephenson, 1918, A, p. 53.

C. parasitica, Couch, 1838, p. 80. (See Gosse, 1860, p. 112; Hertwig, 1879; Faurot, several papers.) (? = *C. rondeletii*, D. Ch., 1828, p. 72.)

C. kroyeri, Dan., 1887, is a synonym of *Allantactis parasitica*.

The British representative of this genus is *C. parasitica*, Couch (= *Sagartia parasitica*, Couch). There can be no doubt that this form really is a *Calliactis* and not a *Sagartia*. It differs from *Sagartia* as represented by the type-species *S. miniata*, *venusta*, etc., by having—

- (i) the cinclides confined to a region a little above the base;
- (ii) only six pairs of perfect mesenteries instead of a larger number;
- (iii) the primary mesenteries sterile instead of fertile.

Apart from this there is a great difference in details and in habit between *C. parasitica* and the typical *Sagartias*, as I can testify from personal experience; and the habitat again (on a shell inhabited by a hermit crab), although not exactly a generic character, is a feature often found in *Calliactis*.

ADAMSIA, Forbes, 1840, p. 181.

Metrididiidae with the body much distorted in the adult so as to form a wrap round a shell inhabited by a hermit crab. The basal disc is greatly extended and secretes a cuticle, formed of solidified mucus, which may extend beyond the mouth of the shell, when the latter becomes too small for the anemone, so as to form not only a support for the anemone but also a house for the crab. Cinclides towards the basal margin of the smooth body; they may be mounted on slight elevations. Oral disc not lobed. Tentacles in more than two cycles in the adult, simple. Sphincter mesogloal. Development of mesenteries may be irregular and asymmetrical.

Species: The genotype, to which the above definition refers, is *A. palliata*, Bohadsch, 1761, p. 136. (See Gosse, 1860, p. 125, and several papers by Faurot.)

AIPTASIA,¹ Gosse, Ann. N.H., 3, i, 416, and 1860, p. 151.

AIPTASIOIDES, Stephenson, 1918, A, p. 51.

Metridiidae with definite base which may vary; it may be well developed; its margin may be irregular, almost "lacerate"; or it may be quite small and weakly adherent, and able to be inflated rather like a physa. Body-form normal but variable, and may attain a long trumpet-shape. Wall delicate, with the cinclides usually in a horizontal zone near the middle of the column. Margin tentaculate. Tentacles simple and smooth, usually non-retractile; may be long, in more than two cycles in the adult, their longitudinal musculature ectodermal. Oral disc simple. Six pairs of perfect mesenteries with diffuse retractors; they may be fertile. Sphincter very weak, mesogloal. Ectodermal longitudinal musculature may be present in body-wall and actinopharynx, at least in the uppermost part.

Species: Genotype, *A. couchi*, Cocks, 1851, p. 11. (See Gosse, 1860, p. 152, and this paper, p. 437.)

Other species are *A. pallida*, Agassiz, 1849 (MS.). (See McMurrich, 1889, Journ. Morph. and Proc. Ac. Nat. Sci. Philad.)

A. sp., McMurrich, 1889, Proc. Acad. Nat. Sci. Philad.

A. prima, Stephenson, 1918 (= *Aiptasioides prima*, Steph., 1918, A, p. 51).

The genus *Aiptasia* as here defined is more limited than it has sometimes been—limited, in fact, to the nearest relatives of the genotype *A. couchi*, the anatomy of which is now definitely described on p. 437. I have excluded from it forms with no mesogloal sphincter, and also forms with specialised tentacles, because although these are closely related to *Aiptasia*, the possession by them of the two characters mentioned seems to necessitate generic separation in the case of the lack of a mesogloal sphincter at any rate. The other character is mentioned again on p. 516, and under *Heteractis*.

AIPTASIMORPHA, n. gen.

AIPTASIA as used for forms without mesogloal sphincters and with smooth tentacles.

¹ It may here be noted that Bourne has suggested classing *Aiptasia* with *Anemonia*. But since it is now known that several *Aiptasias* and relatives have mesogloal sphincters, I take it that this, together with their acontia and cinclides, show their relationships to be with Metridiidae.

Metridiidae with definite base and normal but variable form, which may be like that of a long trumpet or pillar, or may be short. Wall more or less delicate, with cinclides which are typically arranged in a horizontal zone near middle of column, or in horizontal rows in lower parts. Margin tentaculate or with a parapet. Tentacles simple and smooth, in more than two cycles in the adult, probably usually non-retractile, their longitudinal musculature ectodermal. Oral disc simple. Typically six pairs of perfect mesenteries; they may be fertile, and their retractors may be more or less circumscribed. No mesogloal sphincter.

Species: *A. paxi*, n. nom. (*A. couchii*, Pax, 1909, p. 337.) (See this paper, p. 439.)

A. minima, Stephenson, 1918, a, p. 49.

A. leiodactyla, Pax, 1910, p. 198.

A. diaphana, Rapp, 1829.

In 1918 (79, p. 51) I instituted a genus *Aiptasioides* to receive forms resembling *Aiptasia* but with a mesogloal sphincter, following Pax in limiting *Aiptasia* to forms with no sphincter. At that time *A. couchii*, the genotype of *Aiptasia*, had not been anatomically described from British specimens; but now that it has proved (see p. 438) to have a weak mesogloal sphincter, the name *Aiptasia* must apply to the forms which I included in *Aiptasioides* as well as to *A. couchii*, and a new name is required for sphincterless forms. I propose *Aiptasiomorpha*, and confine it at present to forms with smooth tentacles.

HETERACTIS, Milne-Edwards, 1857.

AIPTASIA as used for *A. lucida* by some authors.

Metridiidae with definite base. Cinclides in a horizontal zone near middle of column. Margin tentaculate. Tentacles in probably more than two cycles in the adult, not fully retractile: they possess on their surface a number of scattered spherical or reniform protuberances, which are hollow outpushings of the wall of the tentacle, differing histologically from the rest of the tentacle chiefly in that they possess many nematocysts and have reduced longitudinal musculature. Longitudinal musculature of tentacles ectodermal. Oral disc not lobed. Six pairs of perfect mesenteries. Diffuse retractors. Sphincter weak mesogloal.

Species: *H. lucida*, D. & M., 1860.

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It has seemed best (see p. 516) to separate forms with modified from those with normal tentacles, and this involves the restoration of the genus *Heteractis*. I have defined it to fit *H. lucida*, as described by McMurrich, 1896, p. 182. There remains the difficulty that *H. aurora* is really the type of *Heteractis*, and if this proves to be something different from *H. lucida* the latter will need another name. *Heteractis* differs from *Bartholomea* in that it has a mesogloal sphincter. Pax describes (1910, p. 201) an anemone which he identifies as *lucida*, but it has no sphincter, and from his figure of a tentacle it would seem that the thickenings are rather different from those of McMurrich's species. Perhaps Pax's anemone is something other than *lucida*, and should be included under *Bartholomea* as defined below.

BARTHOLOMEA, Duch. & Mich., 1866.

Aiptasia as used for *A. annulata*, etc.

Metridiidae with definite base. Body-wall delicate, with cinclides typically in a horizontal zone near middle of column, which may be fairly long. Margin tentaculate. Oral disc not lobed. Tentacles in more than two cycles in the adult, their longitudinal musculature ectodermal; they may be long and are not fully retractile. The tentacles have spiral or incompletely annular raised bands on their surface, which are of the nature of batteries of nematocysts; these bands may occur throughout the extent of the tentacle, or near the tip only. Perfect mesenteries, six, seven, or eight pairs. Retractors diffuse, sometimes rather restricted. Primary mesenteries usually sterile. No mesogloal sphincter.

Species: Genotype, *B. annulata*, Lesueur, 1817, p. 172. (See also McMurrich, 1889, Journ. Morph., and Pax, 1910, p. 206.)

B. peruviana, Pax, 1912, p. 18.

? *B. tagetes*, D. & M., 1866, p. 133. (See McMurrich, 1889, Journ. Morph., and Pax, 1910, p. 203.)

In separating from *Aiptasia* forms with specialised tentacles (see p. 516), it has been necessary to revive two old genera—*Heteractis* for forms with a mesogloal sphincter and *Bartholomea* for those with no sphincter. The genus *Bartholomea* was established in 1866 and included *B. solifera* (= *annulata*) and *B. tagetes*. As these are the

two species with which we are mainly concerned at the moment Bartholomea is evidently the right name for them. I have put a query before the name of *B. tagetes* because I am not sure whether it belongs here or in Aiptasiomorpha. McMurrich describes the tentacles as smooth, but Pax states that the thickenings are present but inconspicuous and flat.

Family 5. CHONDRACTINIIDÆ.¹

CHONDRACTININÆ, Haddon, 1889, p. 304.

CHONDRACTININÆ, Haddon, 1898, p. 458.

PHELLINÆ as used by Carlgren, 1893, p. 109, except PHELLIA.

NOT PHELLINÆ, Verrill, 1868.

Actiniina. Definite base, which may be flat and adherent, or may clasp a cylindrical object or form a mud-enclosing cup; more than one of these types may occur in one and the same species. Body-wall variable, frequently tough and cartilaginous and sometimes very thick; may be uninterrupted or may be divided into two regions—a main lower scapus and a submarginal capitulum. These regions may both be smooth; the lower may be encrusted with sand, or the scapus may develop a smaller or larger number of prominent or insignificant tubercles and may also possess cuticle; the capitulum may bear ridges or crests which may break up into tubercles, but it is almost always free from cuticle. No cinclides.² Tentacles simple or with aboral basal swellings of mesogloea, their longitudinal musculature ectodermal or meso-ectodermal. Oral disc simple or bilobed.

¹ There is not now any genus called Chondractinia, since that name has been shown to be a synonym of Hormathia. But that does not provide any reason why the name Chondractiniinae of Haddon should not be used as the foundation of the name of the new family—it is not misleading and is very appropriate to many of the forms included in the family.

² With regard to this it may be noted that although the members of this family have not, so far as we know, any true cinclides, there is at least one record of perforations of the wall which, although probably not really cinclides, were rather curious. An account of these will be found in 80, pp. 144-145.

Mesenteries not divided into macrocnemes and microcnemes. Only six (or rarely a very few more) pairs of mesenteries perfect. Primary mesenteries sterile. Retractors as a rule diffuse, but may be restricted or circumscribed. Acontia present, but may be so reduced as to be rudimentary. Sphincter mesoglæal, usually well developed.

Genera: **HORMATHIA**, **ACTINAUGE**, **PARAPHELLIA**, **SAGARTIOMORPHE**,
LEPTOTEICHUS, **CHONDRODACTIS**, and probably **PHELLIACTIS**.

Other genera of doubtful standing which may possibly find a place here are **AMMONACTIS**, **VERRILL**, **KODIOIDES**, **DAN.**, **ALLANTACTIS**, **DAN.**, **ANTHOSACTIS**, **DAN.**

HORMATHIA, Gosse, Ann. N.H., 3, iii, 47, 1860, p. 218.

TEALIA, Gosse, Ann. N.H., 3, i, 417, 1860, p. 205, pro parte (*T. digitata*).

BUNODES, Gosse, Ann. N.H., 3, ii, 194, 1860, p. 189, pro parte (*B. coronata*).

CEREUS as used by Hertwig, 1882, p. 76 (*C. SPINOSUS*).

NOT **CEREUS**, Oken.

PHELLIA as used by Hertwig, 1882, p. 80 (*P. PECTINATA*), and 1888, p. 24 (*P. SPINIFERA*).

NOT **PHELLIA**, Gosse.

CHONDRACTINIA, Lütken, 1860, p. 190.

CHITONACTIS, Fischer, 1874, p. 226.

CHITONANTHUS, McMurrich, 1893, p. 189.

Chondractiniidæ with variable base, which may be an adherent disc or may form a more or less fully developed cup enclosing mud, or may be long and narrow, clasping a spine-like support, in which case its edges may fuse where they meet; more than one of these types may occur in one and the same species. Body-wall variable, often tough and cartilaginous, sometimes thick. Column divided more or less definitely into scapus and capitulum. Except in small and in rare smooth specimens the scapus possesses at least some development of solid tubercles. These may form one single circle round its distal margin, or they may be more widely distributed; in the latter case they may be without definite arrangement, or there may be a tendency to arrangement in vertical rows, which may be carried out definitely as regards at least some of them, in which case the rows are as a rule in multiples of six, rarely of seven or eight. Typically about twelve (or a multiple) "coronal" tubercles are recognisable where scapus and capitulum join, though they may not be different from the other tubercles and may merge into the ridges of the capitulum; the scapus may or may not be provided

with cuticle. Capitulum nearly always free from cuticle; may be smooth, or may be provided with longitudinal ridges which may be distinct or feebly developed and vary in form, sometimes being broken up into tubercles themselves; they sometimes appear on incipient contraction, being absent in expansion; when present they are most often about twelve (or a multiple) in number. Tentacles simple, in more than two cycles in the adult, their longitudinal musculature ectodermal. Oral disc not lobed; its radial musculature may be partly mesogloal. Typically six pairs of perfect mesenteries, rarely seven or eight pairs. Retractors diffuse, but may be very well developed.

Species: Genotype, *H. margaritae*, Gosse, Ann. N.H., 3, iii, 47, and 1860, p. 219. (See also Haddon, 1889, p. 310.)

Others are *H. andersoni*, Haddon, 1888, p. 251.

H. digitata, Müller, 1776, p. 231. (See Haddon, 1889, p. 306, and Carlgren, 1893, pp. 110 and 138.) (= *Tealia digitata*, Gosse.)

H. coronata, Gosse, Ann. N. H., 3, ii, 194, 1860, p. 202.

H. marioni, Haddon, 1889, p. 313.

H. nodosa, Fabr., 1780, p. 350. (See Haddon, 1889, p. 308, and Carlgren, 1893, pp. 115, 138.)

H. pectinata, Hertwig, 1882, p. 81. (See also McMurrich, 1893, p. 190.) (= *H. spinifera*, Hertwig, 1888, p. 24.)

H. exlex, McMurrich, 1904.

H. castanea, McMurrich, 1904.

H. longicornis, Verrill, 1882, p. 222.

H. spinosa, Hertwig, 1882, p. 76.

The long definition of the above genus will show how variable a one it is in some respects. Moreover, many of the variations mentioned may be exhibited by different specimens of one and the same species, so that generic characters cannot be made of them. McMurrich (1893, p. 209) and Haddon (1898, p. 459) have already pointed out that *Chondractinia* and *Chitonactis* cannot be distinguished from *Hormathia* on the basis of the nature and arrangement of the tubercles. It is also clear that McMurrich's genus *Chitonanthus* cannot stand, since the presence or absence of capitular ridges is not constant for some species (see p. 512). The species assigned to *Phellia* and *Cereus* by Hertwig, moreover, really belong to this genus; Hertwig did not correctly interpret the two genera in question, as has been pointed out before by Haddon and McMurrich. *Bunodes minuta*, Hertwig, has also been placed in *Hormathia* by Haddon.

(1898, p. 459; 1889, p. 312). It is probably a member of this genus, but has only *two* cycles of tentacles and only *two* pairs of perfect sterile mesenteries instead of six. The second of these features may be an individual abnormality or both may be due to the small size of the animal, but I prefer to leave the species out of the genus till more is known of it.

ACTINAUGE, Verrill, 1883, p. 50.

Chondractiniidæ with adherent or mud-clasping base, both sorts found in the same species. Body-wall typically cartilaginous, very thick or very thin according to state of distension, etc. Column divided more or less definitely into scapus and capitulum. Scapus tuberculate, the tubercles with or without cuticle, irregularly arranged or with a tendency to arrangement in vertical rows; coronal tubercles or coronal rows of tubercles about twelve or a multiple of twelve, more or less distinct, sometimes merging into capitular ridges. Capitulum nearly always without cuticle, usually ridged, but not invariably, the ridges very variable in development, typically about twelve or a multiple. Tentacles in more than two cycles in the adult, their longitudinal musculature ectodermal. Each tentacle (or sometimes each tentacle of the inner cycles) has a solid mesogloal swelling on its aboral side at the base; the swellings may be very large, or they may be so reduced as to be almost suppressed, both states occurring in different individuals of one species: but they are always present: there is a definite connection between the ridges of the capitulum and the bases of some of the tentacles—in *A. richardii*, for instance, the ridges appear to be often due to extensions of the basal swellings of the fourth-cycle tentacles which run over the edge of the disc and down the capitulum. Oral disc not lobed. Six pairs of perfect mesenteries. Retractors diffuse, may be well developed.

Species: Genotype, *A. verrillii*, McMurrich, 1893, p. 184. (= *Urticina nodosa*, Verrill, 1873, p. 440.)

A. fastigata, McMurrich, 1893, p. 187. (= *Actinauge nodosa* var. *coronata*, Verrill, 1883.)

A. richardii, Marion, 1882, p. 460. (See Haddon, 1889, p. 319, and Stephenson, 1918, B, pp. 148-154.)

PARAPHELLIA, Haddon, 1889, p. 321. (See Text-figs. 29 and 30.)

Chondractiniidæ with well-developed base which may be widely expanded. Column divided into scapus and capitulum; scapus smooth or slightly corrugated, without cuticle (always?), but sometimes encrusted with sand or with a thin coating of hardened mucus in which sand may be embedded or a thick wrinkled bark-like coating; capitulum

narrow and smooth. Tentacles simple, in more than two cycles in the adult, their longitudinal musculature ectodermal. Oral disc simple, its radial musculature ectodermal. The six pairs of perfect mesenteries have strong circumscribed retractors, whereas those of the second cycle are diffuse. (See Text-figs. 29 and 30.)

Species: *P. expansa*, Haddon, 1886, p. 616, 1889, p. 321. (See Text-figs. 29 and 30.)

The above definition is drawn up so that of the three species which have been referred to the genus *Paraphellia* it includes only the one for which the genus was originally founded (*P. expansa*). I have intentionally excluded the others (*P. lineata* and *P. huntii*) because they seem to me to be sufficiently different from *P. expansa* to claim generic distinction. *P. expansa*, with which I am personally acquainted, is a very distinct form, and its powerful circumscribed retractors are enough in themselves to separate it from forms with diffuse ones. The limits of the genus *Sagartiomorphe*, Kwiet., are not at present very clear, but it would seem that *P. lineata* and *P. huntii* would be better placed there than in *Paraphellia*, and consequently I have included them in *Sagartiomorphe* pending further knowledge. It is not impossible that they will finally need a distinct genus to themselves on account of the nature of the margin.

SAGARTIOMORPHE, Kwietniewski, 1898, p. 396.

PARAPHELLIA, as used by Haddon in 1893, pp. 129-130, pro parte, and in 1898, pp. 460-462, pro parte.

Chondractiniidæ with definite base. Column smooth, without cuticle

TEXT-FIG. 29.

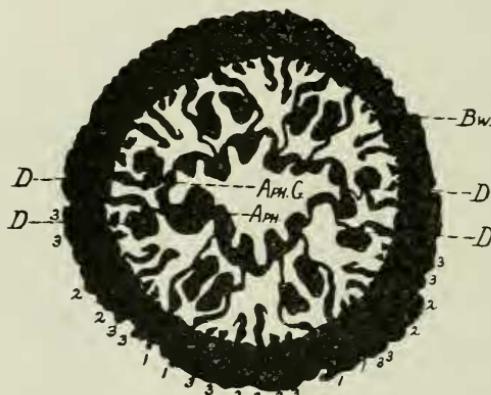


Primary mesentery of *Paraphellia expansa*. *CM*. Endodermal circular musculature. *E*. Endoderm. *F*. Mesogleal processes for muscle. *M*. Mesogloea. *R*. Retractor.

its upper margin may be raised into a fold. Tentacles simple, in more than two cycles in the adult, their longitudinal musculature ectodermal. Oral disc simple, its radial musculature ectodermal. Perfect mesenteries with diffuse retractors.

Species: Genotype, *S. carlgreni*, Kwietniewski, 1898, p. 396. To this I add *S. hunti*, H. & S., 1893, p. 129, 1898, p. 461, and *S. lineata*, H. & S., 1893, p. 130, 1898, p. 462. (See note under *Paraphellia*.)

TEXT-FIG. 30.



Transverse section of body of *Paraphellia expansa*. *APH.* Actinopharynx. *APH.G.* Actinopharyngeal groove. *BW.* Body-wall. *D.* Directive mesentery. Numbers indicate mesentery-cycles.

LEPTOTEICHUS, Stephenson, 1918, A, p. 57.

Chondractiniidae with definite base. Column not divided into scapus and capitulum, smooth, without tubercles or cuticle, with a tentacular margin. The animal may attain large size and firm, tough, very thick wall. Tentacles in more than two cycles in the adult, devoid of basal swellings; they may be large and stout; their longitudinal musculature is almost completely ectodermal, but the radial musculature of the oral disc is partly mesogloal. Oral disc simple. Six pairs of perfect mesenteries with quite diffuse retractors. The processes of the mesenterial musculature may be stout and finger-like. Acontia so much reduced as to be rudimentary.

Species: *L. insignis*, Stephenson, 1918, A, p. 57.

The features which distinguish *Leptoteichus* from *Sagartiomorphe* are not very striking when reduced to

a bare definition. The most definite of them are the rudimentary nature of the acontia in *Leptoteichus* and the partially mesogloœal character of its radial musculature. Its tentaculate margin also marks it off at least from *S. carlgreni*. But a study of *Leptoteichus* "in the flesh" seems to show that it is different in its general make-up from the small *Sagartiomorphe*-forms, and in my belief it merits generic distinction. It is a large deep-water Antarctic form.

CHONDRODACTIS, Wassilieff, 1908.

Chondractiniidæ with base of variable form; it may be adherent, may clasp a spine, or may form a mud-enclosing hollow. Column typically with tough cartilaginous wall which varies, but may be very thick; it may bear rounded or pointed tubercles without very regular arrangement as a rule; there is at least frequently no cuticle; if there is any distinction into scapus and capitulum it is not very well marked; the capitulum may bear irregular ridges: margin tentaculate. Tentacles never in more than two cycles at the margin of the disc, even in the adult; they have thickenings or swellings of mesogloœa on the aboral side at the base; their longitudinal musculature is ectodermal. Oral disc simple or bilobed with the two lobes able to fold up against one another; its radial musculature meso-ectodermal or ectodermal. Six pairs of mesenteries or a very few more are perfect, and the retractors are diffuse or somewhat restricted.

Species: *C. magna*, Wassilieff, 1908.

C. japonica, Wassilieff, 1908.

C. duplicata, Stephenson, 1918, B, p. 142.

C. coccinea, Stephenson, 1918, B, p. 136.

C. pulchra, Stephenson, 1918, B, p. 139.

C. crassa, Wassilieff, 1908, is of doubtful standing since its acontia have not yet been discovered.

PHELLIACTIS, Simon, 1892.

Chondractiniidæ with smooth body-wall. Size may be large and wall may be very thick. Scapus with a very delicate cuticle. All tentacles with a thick abaxial swelling. Capitulum naked.

Species: *P. hertwigi*, Simon, 1892, p. 75.

I am unable to give a full diagnosis of this genus because I could nowhere obtain a copy of the original description of it. The details given are taken from Haddon, 1898, p. 462.

Family 6. ACTINOSCYPHIIDÆ,¹ n. fam.

PARACTIDÆ, as used by some authors, pro parte (e. g. Stuckey, 1909, Carlgren, 1901, McMurrich, 1893, Stephenson, 1918, A and B). NOT part of the original Paraectidæ of Hertwig, 1882.

Actiniina. Definite base of variable form; it may be concave, enclosing mud, or much reduced, or adherent, or may clasp a spine. Body-wall variable, usually smooth, sometimes with small hollow papillæ and partially encrusted. No cinctides. Tentacles simple or with aboral basal swellings, their longitudinal musculature ectodermal. Oral disc simple or undulate or bilobed. Mesenteries not divided into macrocnemes and microcnemes. Only six pairs of perfect mesenteries, and these may be sterile or may bear gonads as well as some or all of the others. Retractors usually diffuse, rarely circumscribed on the primary mesenteries. No acontia. Well-developed or weak mesogloæal sphincter.

Genera: ACTINOSCYPHIA, PARANTHUS, ISOPARACTIS, ? LILLIELLA.

ACTINOSCYPHIA. n. nom. (See Text-fig. 31.)

ACTINERNUS, Verrill, 1879, pro parte.

ACTINERNUS, as used by McMurrich, 1893, for A. PLEBEIUS.

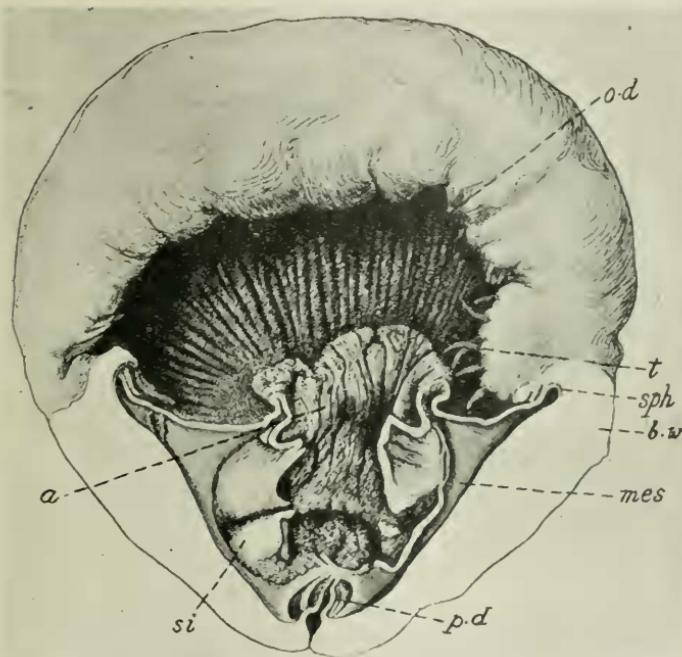
Actinoscyphiidæ with pedal disc of variable extent. It may be adherent, or may be so reduced as to be almost absent; it may be concave, secreting a cuticle and enclosing mud, or may embrace a cylindrical object. Column-wall smooth, sometimes so thick that it forms a jelly-like coating to the body (see Text-fig. 31), so that the general appearance may resemble that of a Scyphozoan. Tentacles in the adult arranged in two cycles only at the margin of the oral disc, and provided with aboral basal swellings of mesogloæa, which, at least in the case of the outer cycle, are continuous with the body-margin.

¹ If it should be thought that this (or indeed any other) family contains forms too widely different from each other as regards general external form and appearance, a study of the genera *Actinoscyphia*, *Actinernus* (*Porponia*), and *Polysiphonia* will help to show how very misleading externals are when it is a case of finding out relationships. These three genera are curiously similar superficially, but anatomically are so different that they belong to three different families—Actinoscyphiidæ, Endocœlactidæ and Paractidæ—and seem quite unrelated to one another. Possibly the deep water habitat accounts for the similarity to some extent. (See p. 488 et seq.)

Longitudinal musculature of tentacles and radial musculature of oral disc entirely ectodermal. Oral disc wide, undulate, or lobed, sometimes bilobed. The six pairs of perfect mesenteries are sterile and have weak diffuse retractors. The animals may attain large size.

Species: Genotype, *A. saginata*, Verrill, Amer. Journ. Sci., 3, xxiii, no. 4, p. 225. (See Stephenson, 1918, B, pp. 127-131.)

TEXT-FIG. 31.



Actinosecyphus aurelia vertically divided, one half of the specimen, showing anatomy. *a.* Actinopharynx. *b.w.* Body-wall. *mes.* Mesentery. *o.d.* Oral disc. *p.d.* Pedal disc. *si.* Actinopharyngeal groove. *sph.* Sphincter. *t.* Tentacle.

A. plebeia, McMurrough, 1893, p. 166.

A. aurelia, Stephenson, 1918, B, p. 131. (See Text-fig. 31.)

In a paper on some Irish Actiniaria (80), published in 1918, I defined the genus *Actinernus*, Verrill, practically as above, pointing out at the same time that the name might

have to be changed if it should prove that the type-species of Verrill's genus (*A. nobilis*) was a *Porponia*. In a paper also published in 1918, but which I did not see till my paper was printed, Carlgren has shown that *A. nobilis* is indeed a *Porponia*, so that the name *Actinernus* must belong to *A. nobilis* and other species like it, and *Porponia* becomes a synonym of it. But *Actinernus* (= *Porponia*) is quite unrelated to the three forms whose specific names are *saginatus*, *plebeius* and *aurelia*, belonging, in fact, to the *Endocœlactidae*. A new name is therefore required for the genus which is to contain the three last species, and I suggest *Actinoscyphia*. The name refers to the cup-like form of body often found in the genus.

PARANTHUS. Andres, 1883, p. 472.

Actinoscyphiidae with definite base. Column smooth; capitular ridges may occur; margin indistinct. Tentacles simple, in more than two cycles in the adult, their longitudinal musculature ectodermal. Oral disc simple. Six pairs of perfect mesenteries which may or may not be fertile and which bear diffuse retractors.

Species: Genotype *P. chromatoderus*, Schm., 1852, p. 15. (See Maguire, 1898.)

♀ *P. lineolatus*. McMurrich, 1893 (= *A. lineolata* ♀, Couthouy in Dana, 1846). (See McMurrich, 1893, p. 162, and McMurrich, 1904.)

♂ *P. nivea*, Lesson. (See McMurrich, 1904.)

I refer the species *lineolatus* with some hesitation to this genus. I am not acquainted with actual specimens of it, but cannot find any very valid reason for excluding it. More study of the species, however, is desirable. But whether it belongs to *Paranthus* or not, it should be placed in the family *Actinoscyphiidae* and removed from the genera *Paractis* and *Pycnanthus*, in both of which it has been placed at different times. Its "capitular ridges" are a character of little value as an indication of relationship (see p. 512), and its six pairs of perfect mesenteries only and its ectodermal longitudinal tentacular musculature quite remove it from *Paractis* and *Pycnanthus*, which have

numerous perfect mesenteries and mesogloœal longitudinal tentacular muscles.

The other species referred with a query to the genus, *P. nivea*, must similarly be removed from *Paractis* because of its ectodermal longitudinal tentacle-muscles, but it is not quite certain whether six pairs of mesenteries or more are perfect; if six, then the species must apparently be reckoned as a *Paranthus*; if numerous pairs, it probably belongs to *Parantheoides*, unless other differences should be demonstrated which will form for it a new genus near one of those just mentioned.

ISOPARACTIS, n. nom.

PARACTIS, as used by Stuckey, 1909, p. 387, and 1913, p. 132, pro parte.

Actinoseyphidiæ with definite base. Smooth body-wall. Tentacles simple, in more than two cycles in the adult, their longitudinal musculature ectodermal. Oral disc simple. Six pairs of perfect mesenteries which bear strong circumscripted retractors and are mostly fertile. The other mesenteries are feebly developed, but are fertile.

Species: *I. ferax*, Stuckey, 1909, p. 387; 1913, p. 132.

The only hitherto recorded species of this genus was originally described by Stuckey (1909, p. 387; 1913, p. 132—corrections of first description in this second paper) as *Paractis ferax*. In re-defining the genera it has been unavoidable to remove it from the genus *Paractis*, and on the sum of its main features it seems to find its place in this family. *Paractis* is a genus the members of which have numerous perfect mesenteries, mesogloœal longitudinal tentacle-muscles and diffuse retractors. In *I. ferax* there are only six pairs of perfect mesenteries, and these bear strong circumscripted retractors and the longitudinal tentacular musculature is ectodermal. I have therefore suggested a new genus, *Isoparactis*, for the species *ferax*.

LILLIELLA, Stephenson, 1918, A, p. 33.

Actinoseyphidiæ (?) with definite base. Column feebly divided into scapus and capitulum, wall thick in the only recorded specimen of the only known species; scapus with poorly developed patchy incrystation.

not a true cuticular sheath. Mesoglæa of scapus contains numerous lacunæ of all shapes and sizes; some of these are so large and so near the surface that they form externally visible hollow papillæ. Tentacles simple, probably in more than two cycles in the adult, their longitudinal musculature probably ectodermal. Oral disc simple. Retractors of the six pairs of perfect mesenteries probably diffuse.

Species: *L. lacunifera*, Stephenson, 1918, A, p. 33.

The position of this genus is as yet uncertain because the only known specimen was too badly preserved to allow of certainty as to presence or absence of acontia. If the latter should be discovered it would go to the Chondractiniidæ.

Family 7. SAGARTIIDÆ, sensu stricto.

SAGARTIADÆ, Gosse, 1858, p. 415. 1860, p. 9, pro parte.

SAGARTINÆ, Verrill, 1869, p. 477, pro parte.

SAGARTINÆ, as used by Carlgren, 1893, p. 87.

SAGARTINÆ, as used by Haddon, 1898, p. 448.

Actiniina. Definite base. Body-wall more or less delicate, without cuticle, pierced by cinclides. Tentacles simple, their longitudinal musculature typically ectodermal. Oral disc simple or undulate. Mesenteries not divided into macrocnemes and microcnemes. Perfect mesenteries more than six pairs (except in very rare exceptional cases), usually numerous, the retractors more often diffuse, frequently strong diffuse. Some at least of the primary mesenteries fertile as well as others. Acontia present. Sphincter mesoglæal, often well developed.

Genera: SAGARTIA, CEREUS, ARTEMIDACTIS.

GEPHYRA, Von Koch, may also come here, and may prove to be simply a small SAGARTIA.

NEMACTIS, M. Edw., may also, possibly, find a place here.

SAGARTIA, Gosse, 1855, 1860, p. 25.

SAGARTIA, Gosse, 1855, pro parte.

SAGARTIA, Gosse, 1860, excluding "S. PARASITICA," which is a CALLIACTIS, and "S. BELLIS," which is CEREUS PEDUNCULATUS, and probably S. (?) CHRYSOSPLENUM. Including CYLISTA, Gosse, 1860, p. 123, and THOE, Gosse, 1860, p. 122.

Sagartiidæ with definite base. This is not always used for adherence,

and the animal may live free for a time or buried in mud or sand. Column soft and smooth, but for minute corrugations which may disappear on distension, and for suckers which are present in some species and may be capable of attaching foreign objects to themselves. Margin tentaculate. Cinclides scattered in certain parts of the body or generally distributed; they may be endodermal evaginations or ectodermal invaginations (see pp. 451-455); both kinds may occur in one animal: they are not always actual perforations, but may be very thin places definitely organised (see pp. 454-455). Tentacles simple, not especially numerous, in more than two cycles in the adult, their longitudinal musculature ectodermal; their arrangement may be hexamerous, pentamerous, heptamerous, octamerous or irregular. Oral disc not lobed, though it may be rather undulate in some specimens of a species at certain times, and not widely expanded, though it may be broad and somewhat exceeding the middle part of the column; its radial musculature ectodermal. Gonads appear on mesenteries of the first cycle as well as others. Number of perfect mesenteries variable; twelve pairs or more typically, but sometimes fewer; their arrangement may be hexamerous, pentamerous, heptamerous, octamerous or irregular. Retractors vary from weak diffuse to powerful diffuse or even somewhat circumscribed.

Species: Genotype, *S. MINIATA*, Gosse, 1853, p. 127; 1860, p. 41. (See this paper, p. 439.)

S. venusta, Gosse, and *S. NIVEA*, Gosse, are near relations.

S. viduata and *S. undata*, Müller, are described anatomically by Carlgren, 1893.

Species numerous.

Sagartia is a genus needing special study in itself. A large number of forms have been assigned to it, but the anatomy of some of them is insufficiently known. It is quite likely that when more is known of some of these they will be removed from the genus and placed in one of the genera of the Choriactidae or Chondractiniidae. It is quite possible, for instance, to have a form externally like *Sagartia*, but differing anatomically by having no cinclides or by having a different arrangement of mesenteries. It is also possible that *Sagartia* itself, when adventitious forms have been removed from it, may need subdivision, but at present we hardly know enough about the structure of cinclides and retractor muscles, and so on, in the genus to make any change. It is seen, however (see p. 455), that two different kinds of

cinclides may occur in one and the same specimen of a species. I have not accepted the subdivision of the genus sometimes made into *Sagartia*, *Thoe* and *Cylista*, because intimate acquaintance with living representatives of all three has convinced me that it would be unwise to do so unless marked anatomical differences should subsequently turn up. Carlgren (1893, p. 88) has already ranked them as synonyms of *Sagartia*.

CEREUS, Oken, 1815, p. 349.

HELIACTIS, Thompson, 1858 (P. Z. S., xxvi, p. 145, and A. M. N. H. (3), ii, p. 229).

SCYPHIA, Gosse, 1860, p. 123.

Sagartiidae with definite base. Column soft and smooth but for minor corrugations, with suckers capable of attaching foreign bodies to themselves. Cinclides scattered. Margin tentaculate. Tentacles simple, numerous, in more than two cycles in the adult. Oral disc variable in form, but capable of widely exceeding the rest of the body; the lower part of the column is sometimes elongate and stem-like (though by no means always), and the upper part expands to meet the edge of the disc; the latter may be flat and circular or vase-like or undulate, but not permanently lobed. Gonads appear on primary as well as other mesenteries, and ova and spermatozoa may occur in one and the same mesentery at the same level. Retractors well developed, diffuse.

Species: The above definition applies to the genotype, *C. pedunculatus*, Pennant, 'Br. Zool.', iv, 102. See also Gosse, 1860, p. 27, and Haddon, 1889, p. 302, and 1898, p. 451. (Synonym, *Sagartia bellis*, Ellis, 'Zooph.' 2, Gosse, 1860, p. 27.)

ARTEMIDACTIS, Stephenson, 1918, a, p. 40.

Sagartiidae with definite base. Wall smooth for the most part, delicate for the size of the animal (which may be large), sometimes with slight and inconspicuous nodulations near the margin. Column cylindrical below, but widely expanded above so that the oral disc greatly exceeds the column, though it is not lobed. No definite verrucae or collar, but the margin is more or less distinct and may form a distinct parapet. Cinclides irregularly distributed. Tentacles simple, numerous, in several cycles in the adult, their longitudinal musculature ectodermal. Musculature of mesenteries weak and forming no distinct retractors; its processes, in the one recorded species, thick and lobe-like. Mesenteries of all cycles bear gonads. In the recorded species the mesenterial filament of each mesentery is confined to a certain definite area, variable

in position according to cycle, above and below which the edge of the mesentery is quite free, except in the case of the numerous perfect mesenteries, where part of it may be attached to the actinopharynx.

Species: *A. victrix*, Stephenson, 1918, A, p. 41.

This genus is not altogether dissimilar from *Sagartia* and *Cereus*, but the aggregation of small differences makes it a very distinct form, easily recognised. In its expanded disc it resembles *Cereus*, but in its feeble mesenterial musculature is quite unlike it. Its body-margin is also more distinct than in either of the other two genera, and may form a distinct parapet—perhaps would always do so in life. It is a large animal living in deep water. The distribution of its mesenterial filaments, though not confined to this genus, is curious.

Family 8. CHORIACTIDÆ. n. fam.

SAGARTINÆ as used by McMurrich, 1904, pro parte.

METRIDIINÆ as used by Haddon, 1898, pro parte.

Actiniina. Definite base. Body-wall may be somewhat cartilaginous, may be smooth or tubercled but lacks cinclides; cuticle present or absent. Tentacles simple, their longitudinal musculature typically ectodermal. Oral disc simple, may be somewhat undulate. Mesenteries not divided into macrocnemes and microcnemes. More than six pairs of mesenteries perfect, usually twelve or more pairs perfect. Gonads probably not borne by primary mesenteries. Retractors diffuse. Acontia present. Sphincter mesogloæal.

Genera: *CHORIACTIS* and probably *MITACTIS*.

CHORIACTIS, McMurrich, 1904.

Choriactidæ with definite base. No cuticle. Column may be thick-walled, and may be more or less tuberculated, the tubercles arranged as ridges in the upper part, or there may be simply ridges, and the tubercles may be almost wanting in small specimens. Margin tentaculate. Tentacles simple, in more than two cycles in the adult, their longitudinal musculature ectodermal. Oral disc not lobed, its radial musculature ectodermal. Retractors diffuse. In the only recorded species which had developed gonads, these were absent from the mesenteries of the two oldest cycles.

Species: Genotype. *C. impatiens*. Couthouy in Dana, 1849, McMurrich, 1904.

C. crassa, McMurrich, 1904, is the only other known species.

MITACTIS, Haddon & Duerden, 1896, p. 162.

Choriactidae with definite base. Column smooth, with cuticle. Tentacles simple, in more than two cycles in the adult. Retractors diffuse. Oral disc not lobed.

Species: *M. australiae*, Haddon & Duerden, 1896, p. 162.

M. similis, Haddon & Duerden, 1896, p. 163.

This genus is not yet fully described but probably its position is here, and I therefore include it tentatively in the Choriactidae.

Family 9. **PARACTIDÆ**. Hertwig, *sensu stricto*.

PARACTIDÆ, Hertwig, 1882, p. 41.

ACTINOSTOLIDÆ + **PARACTIDÆ**, *pro parte*, Carlgren, 1893, pp. 64 and 137.

PARACTIDÆ as used by various authors, *pro parte* (e.g. McMurrich, 1893 and 1904; Stuckey, 1909; Stephenson, 1918 A and B).

Including **LIPONEMIDÆ**, Hertwig, 1882, p. 63, *pro parte*.

Including **SICYONIDÆ**, Hertwig, 1882, p. 97, as applied to *Sicyonis*.

Actiniina. A definite but variable base which may be adherent, may be concave and clasp mud. Body-wall thick or thin, often cartilaginous, smooth or ridged or tuberculated or verrucose; margin tentaculate or well marked, sometimes provided with a collar. No cinclides. Tentacles simple or with thickening of the mesoglæa of the base or with aboral basal swellings of mesoglæa; longitudinal musculature typically entirely mesogloal, but may be meso-ectodermal or even ectodermal, and may be reduced or absent in part of each tentacle. Oral disc simple or lobed or undulate. Mesenteries not divided into macrocnemes and microcnemes. Perfect mesenteries more than six pairs, usually numerous. They may or may not bear gonads, and their retractors, though rarely circumscribed, are usually diffuse. No acontia. Sphincter mesogloal, often well developed.

Genera: *PARACTIS*, *CYMBACTIS*, *HORMOSOMA*, *ALLOACTIS*, *ANTHOLOBA*, *TEALIDIUM*, *PARANTHEOIDES*, *SICYONIS*, *ACTINOSTOLA*, *CATADIOMENE*, *STOMPHIA*, *OPHIODISCUS*, *POLYSIPHONIA*, and probably *PSEUDOPARACTIS*.

Some doubtful genera which may possibly be included here in the future are *Raphactis*, Verrill; *Archactis*, Verrill; *Ammophilactis*, Verrill; *Paractinia*, Andres; *Cadosactis*, Dan.; *Cyathactis*, Dan.; *Korenia*, Dan.; *Aulorchis*, Hertw.

It is possible to divide the Paractidae into three sub-families, based on certain curious methods of mesenterial development. These families are:

(1) *Paractinæ*: In this sub-family the mesenteries of one and the same pair are about equally developed, or if any inequality occurs it is irregularly developed.

(2) *Actinostolinæ*: Here the mesenteries of the youngest cycles are usually unequally developed, one partner in each pair being larger than the other in such a way that that partner is always the larger which stands furthest away from the adjacent mesenterial pair of the next oldest cycle.

(3) *Polysiphoniinæ*: In this case the twelve oldest pairs of mesenteries are developed in the ordinary way, but the rest are peculiarly arranged. In each of the exocœls between the primary and secondary pairs the younger mesenteries have a bilateral arrangement, the youngest ones appearing in the middle of the exocœl. Each of these later pairs consists of one larger and one smaller partner, and the oldest of the larger partners are perfect as well as the primary and secondary mesenteries.

If this arrangement of sub-families be adopted, it is found that of the genera enumerated above *Polysiphonia* belongs to the third sub-family, *Actinostola*, *Catadiomene*, *Stomphia* and *Ophioidiscus* to the second, and the other genera to the first. There is not, so far as I can see, any objection to these three groups as sub-families, though I do not think they ought to rank as families. It may be found, however, when more work has been done on the subject, that between the *Paractinæ* and *Actinostolinæ* at least it will not

be possible to draw a hard and fast line, the one merging into the other. This possibility has been suggested to me by a certain amount of work which I have done in connection with it, but I have merely the indication, and cannot as yet speak definitely one way or the other. Inequality of mesenteries, more or less regularly developed, is not confined to the Paractidæ, however.

PARACTIS. Milne-Edwards, 1857, tome i, p. 248.

Paractidæ (Paractinæ) with definite base. Column smooth, with a marginal collar: it may be thin-walled. Tentacles simple, in more than two cycles in the adult, their longitudinal musculature mesogloœal. Oral disc simple, its radial musculature mesogloœal. Perfect mesenteries with diffuse retractors: they may be fertile.

Species: *P. papaver*, Drayton in Dana, 1846, p. 143. (See Clubb, 1908, p. 3.)

A question which presents considerable difficulty is this: What is the genus *Paractis*? Milne Edwards (1857, tome i, p. 248) defines it on external characters as follows:

“Les Paractis ont, comme les Actinies proprement dites, le corps dépourvu de verrues et les tentacules rétractiles; mais ils sont dépourvus de tubercules calicinaux. On voit par conséquent que ce genre est avec les Actinies dans les mêmes relations que les *Anemonia* avec les *Comactis*. Ses tentacules sont presque égaux et médiocrement nombreux. Enfin, le disque calicinal est circulaire.”

An anemone eligible for this genus should therefore have smooth body without acrorhagi, a non-lobed disc, and retractile tentacles not exceptionally numerous. This description, however, would apply equally to different forms, not related to each other, and with quite different anatomy—e. g. to *Epiactis* and *Stomphia*. Since the definition does not indicate anatomy, the only way of getting at a more precise one is by referring to the actual species included by Milne-Edwards in the genus. The first four species which he mentions, in his order, are *P. impatiens*, *P. monilifera*, *P. lineolata*, *P. papaver*. *P. impatiens* has been anatomically described by McMurrich (1904) who found that it

had acontia. Milne-Edwards can hardly have intended to include acontia-possessing forms in his genus, or he would not have excluded it from his *Actinines perforées*, so McMurrich removed *P. impatiens* from it and called it *Choriactis* (see p. 547). *P. monilifera* seems to have some kind of marginal tubercles which make its position as a true *Paractis* untenable, and as far as I know its anatomy is undescribed. As to *P. lineolata* and *P. papaver*, both have been anatomically described, and either would serve as a genotype, but the two are quite different, and it is a case of choosing the right one.

Meanwhile Hertwig (1882, p. 41) set up a family *Paractidæ*, defined as possessing a mesogloal sphincter and numerous perfect mesenteries. It is distinguished from any *Sagartids*, of course, by lack of acontia and cinclides. Of the two species *lineolata* and *papaver*, the second would come within the scope of Hertwig's family, the first would not, nor would it come within the *Paractidæ* as defined in this paper. It seems therefore the best policy to adopt *P. papaver* as the genotype, since it would cause great confusion and readjustment of names to alter the sense of Hertwig's family now. I have therefore drawn up my definition of *Paractis* to fit *P. papaver*, the anatomy of which was described by Clubb, 1908, p. 3. It may need a little modification for the inclusion of other species in the future, but should not be much widened. The possession of mesogloal longitudinal tentacular musculature and of a collar, in addition to its numerous perfect mesenteries, are very definite features. The collar is certainly a feature absent from Milne-Edwards' definition, but it does not in any way contradict the sense of his genus; and since one is bound to define the genus on the basis of *one* of the originally included species, *P. papaver* clearly fulfils the requirements better than either of the three mentioned before it. It seems best also to select the first *suitable* species named in order by the author of a genus, if the actual first one or more are ineligible. The acceptance of *P. papaver* as the genotype of *Paractis*

will necessitate the removal from the genus of a number of other species which have been assigned to it from time to time before its boundaries were strictly enough limited, and which neither agree with each other or with *P. papaver*. This should really be an advantage, and tend to better represent the true relationships of the forms in question. Firstly, *P. excavata*, which is too aberrant a form as regards its tentacles to have ever been placed in *Paractis*, goes to *Alloactis*. *P. lineolata* and *P. nivea* probably find their place in *Paranthus*. *P. tenuicollis* requires a new genus (see *Pseudoparactis*). *P. ignota* is a *Parantheoides* and *P. polaris* apparently a *Cymbactis*. *P. ferax* goes to *Isoparactis*. Further notes regarding these species will be found under the genera mentioned. Other species assigned to *Paractis*, the anatomy of which is not yet known, await definite allocation.

An interesting form has been described by Stuckey (84) as *Paractis fleuri*. He does not describe the position of the longitudinal tentacular muscles, so that the form is hard to allocate. I do not think it comes under *Paractis* as here understood. Its sphincter is most remarkable—mesogloal, but strongly circumscribed. Whether it will be the representative of a new genus, or whether it will fit into one of those here defined, I leave an open question for the present, pending further knowledge.

CYMBACTIS, McMurrich, 1893, p. 174.

PYCNANTHUS, McMurrich, 1893, p. 172.

PARACTIS as used by Clubb, 1908, p. 3. *pro parte*.

Paractidæ (*Paractinæ*) with definite base, which may be adherent or may form a mud-clasping cup. Column smooth but for capitular ridges in some cases; margin tentaculate and without a collar; wall variable, but may be very thick. Tentacles in more than two cycles in the adult, simple or somewhat thickened at the base, their longitudinal musculature mesogloal. Oral disc simple, its radial musculature mesogloal. Retractors diffuse. Older mesenteries may be fertile or sterile.

Species: Genotype, *C. fæculenta*, McMurrich, 1893, p. 174.

Other species: *C. maliformis*, McMurrich, 1893, p. 172.

C. actinostoloides, Wassilieff, 1908.
C. maxima, Wassilieff, 1908.
C. polaris, Clubb, 1908, p. 3.
C. gossei, Stephenson, 1918, B, p. 123.

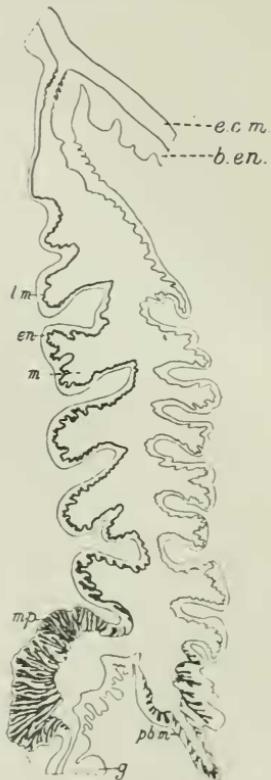
McMurrich established a separate genus, *Pycnanthus*, for *C. maliformis*, which differed from *Cymbactis* as originally defined by possessing capitular ridges. As I have endeavoured to show above (p. 512) the development of these ridges is too variable to form a good generic character, and the genera are here fused.

C. gossei has irregular ridges in contraction which would probably disappear on expansion. *C. polaris* was originally assigned to *Paractis* by Clubb, but the revision of that genus as above makes its transference necessary, since it possesses no collar. The thickened tentacle-bases in *C. gossei* are not quite like the ordinary aboreal basal swellings found in some genera. Although the thickening may be least marked on the oral side, it generally affects the basal part of the tentacle all round, at least to some extent, and hardly seems definite enough to require the generic separation of *C. gossei*. At any rate I leave it for the present.

HORMOSOMA. Stephenson, 1918, A, p. 29. (See Text-fig. 32.)

Paractidae (Paractinæ) with definite base. Body-wall smooth (and in

TEXT-FIG. 32.



Mesentery of *Hormosoma scotti*. *b.en.* Body-wall endoderm. *e.c.m.* Endodermal circular musculature. *en.* Endoderm. *g.* Gonad. *l.m.* Longitudinal musculature. *m.* Mesogloea. *m.p.* Mesogloal processes for muscle. *p.h.m.* Parietobasilar muscle.

the only recorded species thick), without verrucæ or ridges, but with a prominent marginal collar which laps back over the column in expansion. Tentacles simple, in more than two cycles in the adult, their longitudinal musculature mesoglœal. Oral disc simple, its radial musculature mesoglœal. Mesenteries of all cycles fertile. The larger mesenteries with more or less circumscribed retractors, and in the only recorded species with curious ridges also, which support musculature (Text-fig. 32).

Species: *H. scotti*, Stephenson, 1918, a. p. 29 (see Text-fig. 32).

ALLOACTIS, Verrill, 1899, p. 206.

PARACTIS as used by Hertwig for *P. excavata* (1882, p. 41).

Paractidæ (Paractinæ) with definite base. Wall smooth, may be longitudinally furrowed, margin tentaculate, no collar. Tentacles of the adult in two cycles only, their longitudinal musculature reduced on the aboral side, probably even absent at the base, chiefly mesoglœal. Oral disc simple, its radial musculature principally mesoglœal. Mesenteries of all cycles fertile.

Species: *A. excavata*, Hertwig, 1882, p. 41.

Hertwig described the anemone above diagnosed as *Paractis excavata*. Later on Verrill (1899) showed that it was hardly correct to assign a somewhat curious form like this to the genus *Paractis*, which was meant for plain forms; he suggested for it a new genus, *Alloactis*, which I have here adopted. The peculiar constitution of the tentacles and their arrangement in two cycles only in the adult and its lack of a collar cut it off from *Paractis* as represented by *P. papaver* (see above).

ANTHOLOBA, Hertwig, 1882, p. 53.

METRIDIUM, Milne-Edwards, Hist. des corall., tome i. p. 252, pro parte.

Paractidæ (Paractinæ) with definite base. Wall smooth but for reticulations which may be present, margin unspecialised. Tentacles in more than two cycles in the adult, simple, very numerous, their longitudinal musculature (ectodermal to) mesoglœal. Oral disc lobed, its radial musculature chiefly mesoglœal. At least twenty-four pairs of perfect mesenteries, the primaries and some others sterile, the retractors diffuse, hardly specialised. Sphincter very long.

Species: Genotype, *A. reticulata*, Couthouy in Dana, 1846, p. 144. (= *A. achates*, Drayton, 1846.)

TEALIDIUM, Hertwig, 1882, p. 51.

Paractidae (Paractinæ) with definite base. Column with papillæ or with vertical rows of verrucæ which may attack foreign bodies; with a circular swelling just below the crown of tentacles, in expansion at least. Tentacles simple, in more than two cycles except in small specimens, their longitudinal musculature ectodermal. Oral disc simple, its radial musculature ectodermal. Mesenteries all perfect and mesenteries of all cycles fertile except sometimes the directives.

Species: *T. cingulatum*, Hertwig, 1882, p. 51 (genotype).

T. cinctum, Stuckey, 1909, p. 389.

Further knowledge of this genus may perhaps result in its division into two genera, distinguished by structure and arrangement of the papillæ or verrucæ. I have included the statement that the tentacles are in more than two cycles except in small specimens, because in *T. cinctum*, which is of medium size, the tentacles are apparently in four cycles; and it seems very probable that the reason why there are only two cycles in *T. cingulatum* is that it is very small. It does not seem to be one of those cases (see p. 514) in which the tentacles never arrange themselves in more than two cycles however large the animal may grow.

PARANTHEOIDES, Carlgren, 1899, p. 28.

PARACTIS as used by McMurrich, 1904, pro parte.

DYSACTIS as used by Hertwig, 1882, p. 44, pro parte.

Paractidae (Paractinæ) with definite base. Column smooth, margin indistinct. Tentacles simple, in more than two cycles in the adult, their longitudinal musculature ectodermal. Oral disc simple, its radial musculature ectodermal. The primary mesenteries may be fertile. Retractors diffuse, at least in *P. ignota*.

Species: Genotype, *P. crassa*, Carlgren, 1899, p. 28.

Others: *P. ignota*, McMurrich, 1904.

P. rhodora, Couthouy in Dana, 1846, p. 148. (See Hertwig, 1882, p. 49.)

Carlgren founded this genus for *P. crassa*, but there seems no doubt that the other species mentioned should also be included. *P. ignota* was assigned by McMurrich (1904) to Paractis, but it differs from that genus as now limited (p. 550) by having the longitudinal tentacular musculature

ectodermal instead of mesogloal. *P. rhodora* was included in *Dysactis* by Hertwig, but as McMurrich (1893, p. 169) showed, the genus *Dysactis* was probably erected for anemones with acontia, and therefore could not be used for Hertwig's species. Of the two species referred by Hertwig to the genus, one has been shown to be an *Actinostola* (McMurrich, 1893, pp. 169 and 209), and the other is *rhodora*, which may fairly be included in *Parantheoides*.

SICYONIS, Hertwig, 1882, p. 98.

Paractidae (Paraetinae) with definite base. Column smooth; may be fairly thick: margin tentaculate. Tentacles in two cycles only in the adult, octamerously arranged, thickened all round at their bases, their longitudinal musculature mesogloal. Each tentacle consists of a thickened proximal part with longitudinal musculature in its mesogloea, and a thinner distal rim without longitudinal musculature and with an unusually large terminal opening; the longitudinal musculature, furthermore, is reduced on the aboral side of each tentacle. Oral disc simple, its radial musculature mesogloal. In the only recorded species there are sixteen pairs of perfect mesenteries, and these are sterile and muscular, their retractors diffuse. Only the mesenteries of the last cycle bear gonads, and these are feebly muscular.

Species: *S. crassa*, Hertwig, 1882, p. 98.

S. elongata, Hertwig, 1888, p. 33.

There does not seem to be any very valid reason why this genus should not rank as a Paractid, judging by Hertwig's account of its anatomy. The tribe in which Hertwig placed it (Paractiniae) has been discarded, and the genus exhibits the essential Paractid features. The curious structure and wide terminal openings of the octamerously arranged tentacles, and their limitation to two cycles only, although there are four cycles of mesenteries, distinguish it from *Cymbactis*, though some features of the tentacle-structure remind one of *C. gossei*. The large terminal openings of the tentacles do not seem to be a feature of any great importance, and it is difficult to know how far they may be due to state and method of preservation.

PSEUDOPARACTIS, n. nom.

Paractidae (Paraetinae) (?) with definite base. Column divided into a thinner upper part or capitulum which is smooth, and a thicker

lower part or scapus which may bear longitudinal ridges which may terminate rather abruptly above. Margin tentaculate, tentacles probably in more than two cycles in the adult. There is a weak sphincter in the capitulum, and apparently a second sphincter in the upper part of the scapus. Longitudinal musculature of tentacles ectodermal. Retractors diffuse.

Species: *P. tenuicollis*, McMurrich, 1904, p. 243.

It seems that the species described by McMurrich as *Paractis tenuicollis* (1904, p. 243) requires generic separation on account of the division of its body into scapus and capitulum, and the possession, apparently, of two sphincters, both mesogloal. It is quite distinct from *Paractis*, both in this respect and in its ectodermal longitudinal tentacular muscle and lack of a collar. Unfortunately there is no statement made with regard to the number of its perfect mesenteries, so that whether it should be included here or in the *Actinoscyphiidae* is uncertain.

ACTINOSTOLA, Verrill, 1883.

Paractidæ (*Actinostolinae*) with definite base, which may be adherent or may form a mud-enclosing hollow. Wall smooth or wrinkled or more or less tuberculated; it may be very thick; margin tentaculate. Tentacles in more than two cycles in the adult, hexamerously arranged, often short and stumpy, simple, their longitudinal musculature mesogloal. Oral disc simple or somewhat undulate but not actually lobed, its radial musculature mesogloal. Primary mesenteries at least sterile. Mesenteries hexamerous. Retractors diffuse. In the youngest cycles the mesenteries of each pair are unequally developed in such a way that the partner furthest away from the adjacent mesenterial pair of the next oldest cycle is the larger.

Species: Genotype, *A. callosa*, Verrill, 1882, pp. 224, 315. (See Carlgren, 1893, p. 71; McMurrich, 1893, p. 167.)

Others are: *A. abyssorum* (Dan.?), Carlgren, 1893, p. 66. (*? Bunodes abyssorum*, Dan.).

A. excelsa, McMurrich, 1893, p. 170.

A. pergamantacea, McMurrich, 1893, p. 171.

A. spetzbergensis, Carlgren, 1893, p. 76.

A. chilensis, McMurrich, 1904, p. 217. (See Clubb, 1908, p. 4.)

A. sibirica, Carlgren, 1901.

A. walteri, Kwietniewski, 1898.

A. crassicornis, Hertwig, 1882, p. 44.

? A. grænlandica, Carlgren, 1893.

CATADIOMENE, n. nom.

ACTINOSTOLA as used by Carlgren, 1899, Wassilieff, 1908, and Stephenson, 1918, b. pro parte.

Paractidæ (Actinostolineæ) with definite base. Column wrinkled or more or less tuberculated or irregularly ridged: it may be very thick-walled: margin tentaculate. Tentacles in more than two cycles in the adult, hexamerously arranged, with swellings of the mesoglœa on the aboral side at the base: they may be short and stumpy and their longitudinal musculature is mesoglœal. Oral disc simple or undulate but not lobed, its radial musculature mesoglœal. Primary mesenteries at least sterile. Retractors diffuse. In the youngest cycles the mesenteries of each pair are unequally developed in such a way that the partner furthest away from the adjacent mesenterial pair of the next oldest cycle is the larger.

Species: *C. atrostoma*, Stephenson, 1918, b. p. 118.

C. carlgreni, Wassilieff, 1908.

C. intermedia, Carlgren, 1899.

It has seemed necessary to establish a new genus for those forms hitherto included in *Actinostola*, which differ from the typical forms in that genus by possessing basal swellings to their tentacles. *Actinauge* and *Hormathia* and other genera are mainly distinguished from each other in a similar way. The possession of the basal swellings is an apparently stable and well-marked feature and a very convenient generic distinction (see p. 516).

STOMPHIA, Gosse, Ann. Nat. Hist. 3, iii, 48, 1860, p. 221.

Paractidæ (Actinostolineæ) with definite base. Body-wall smooth and with tentaculate margin, but varying in thickness: it may be quite thin or quite thick or intermediate. Tentacles simple, in more than two cycles in the adult; their longitudinal musculature is mesoglœal, but there may be an ectodermal muscle-fringe as well as, and quite distinct from, the true mesoglœal musculature. Oral disc simple, its radial musculature mesoglœal. Tentacles and mesenteries frequently arranged octamerously (16-16-32). Perfect mesenteries sterile. Retractors well developed, diffuse. In the youngest cycle or cycles the mesenteries of one and the same pair are unequally developed in such a way that the partner furthest away from the adjacent mesenterial pair of the next oldest cycle is the larger.

Species: Genotype, *S. churchiae*, Gosse, Ann. Nat. Hist., 3, iii, 48. (See Gosse, 1860, p. 222, Carlgren, 1893, p. 80, Stephenson, 1918, b. p. 126.)

Others: *S. selaginella*, Stephenson, 1918, a, p. 36.

?? *S. vinosa*, McMurrich, 1893, p. 163.

I first described in 1918 (a, p. 36) a new Antarctic anemone under the name *Cymbactis selaginella*, one of my chief reasons for referring it to *Cymbactis* being its thick body-wall. But more recently I have been convinced (see p. 513) that there are too many grades of thickness in body-walls for this to be a valid feature for distinguishing genera. Since describing *selaginella*, also, I have had an opportunity of studying the type-species of this genus (*S. churchiae*), and was surprised to find a striking similarity in structure between the two, which is sufficiently marked to make it evident that they belong to the same genus. My sections of *S. selaginella* show indications that the youngest mesenteries probably conform to the *Actinostolinae* rule. They have in common certain features of general facies (when preserved); both have tentacles which can be short and thick and are generally arranged in three cycles on the 16-16-32 plan. There are sixteen pairs of perfect sterile mesenteries in both, and a comparative study of the mesenterial, tentacular and sphincter muscles reveals a good deal of similarity, though at the same time there is quite enough difference for *specific* distinction all the way through.

While referring to *Stomphia* I must correct an error into which I fell with regard to *S. churchiae* in my 1918 b paper, p. 127. I there stated that after careful investigation of two animals I could not satisfy myself that the *Actinostola*-rule was carried out with any definiteness in *Stomphia*, although it held good for some sectors of the animal. I have had occasion to deal further with *Stomphia* since then, and sections of two whole individuals have proved that I was wrong and that the rule is indeed carried out almost exactly. I was misled before by relying too much on dissection.

I include very tentatively *Paractis vinosa*, McMurrich, as a possible *Stomphia*. It has the mesogloal disc and tentacle-muscles and sixteen pairs of perfect sterile mesenteries, but on the other hand we do not know whether its

small mesenteries conform to the Stomphia-rule, and its mesenterial musculature does not seem much like that of the other two.

OPHIODISCUS. Hertwig, 1882, p. 56.

Paractidae (Actinostolinae) with definite base. Column smooth, margin tentaculate. Tentacles simple, in a single corona, their longitudinal musculature mesogloal and confined to the inner or adoral face of each tentacle. Oral disc simple, its radial musculature mesogloal. The larger mesenteries are sterile and possess slightly developed musculature and the gonads are borne on the small unmuscular mesenteries of the youngest cycle. These young mesenteries are also unequally developed, in such a way that in each pair the partner furthest away from the adjacent mesenterial pair of the next oldest cycle is the larger.

Species: *O. annulatus*, Hertwig, 1882, p. 57.

O. sulcatus, Hertwig, 1882, p. 61.

I have restored the genus *Ophiodiscus* to the position in the Paractidae originally assigned to it by Hertwig, because there does not seem to me to be adequate ground for placing it elsewhere. McMurrich has placed it in the Dendromeliidae on the strength of a pseudo-tentacle which was supposed to have been connected with it—the possession of pseudo-tentacles being a diagnostic character of that family.

But I submit that there is no definite evidence that *Ophiodiscus* has any pseudo-tentacles, even though it cannot be actually stated that it has not. Hertwig says that there was *one* "pseudo-tentacle" enveloped in the same piece of cloth as *four* specimens of *Ophiodiscus*. In the first place this does not imply any connection between the pseudo-tentacle and the anemones. If I may mention an instance from my own experience, in a collection of anemones which I described, one bottle containing anemones had in it also a fine branched body which at first sight looked like a branched tentacle, but which on sectionising proved to be an Aleyonarian. My point is that there may have been no more connection between the *Ophiodisci* and the pseudo-tentacle than there was between my anemones and Aleyonarian. Again, there would surely have been more than one pseudo-

tentacle among four *Ophiodisci* if it had really belonged to them, and Hertwig expresses his inability to find any pseudo-tentacle remains *on* the anemones. Another point is that the pseudo-tentacle in question had *circularly* arranged muscle-fibres in its *ectoderm*, and *longitudinal* fibres, also apparently muscular, in its *endoderm*. This arrangement is very difficult to account for if the pseudo-tentacle were an outgrowth of an anemone, in which case, according to ordinary rules, the *endoderm* should possess circular muscle and the *ectoderm* either no muscle-fibres or longitudinal ones. In *Lebrunia danaë*, which has genuine pseudo-tentacles, the endodermal musculature of the latter is, indeed, as one would expect, part of the endodermal circular muscle of the body-wall and its fibres run circularly.¹

On these grounds I am inclined to think that the stray “pseudo-tentacle” had nothing to do with the *Ophiodisci*.

But be this as it may—and nothing but fresh and sufficiently well-preserved material can finally settle it—on its other characters *Ophiodiscus* is a Paractid, judged by Hertwig’s account. It has pedal disc, numerous perfect mesenteries not divided into macrocnemes and microcnemes, mesoglœal sphincter, no acontia or cinclides, mesoglœal disc and tentacle musculature, and even exhibits the tendency, which I have mentioned elsewhere (p. 492), of the younger mesenteries to produce the gonads in higher anemones in its extreme form. It also exhibits an unequal development of the small mesenteries similar to that which prevails in *Actinostola*, *Cata-*

¹ This statement is made after consulting Pax, 1910, pp. 213–214. But I see that McMurrich, 1889 ('Journ. Morph.') describes what seems to be longitudinal musculature in the endoderm of the pseudo-tentacles of *L. neglecta*. He describes no circular fibres in the ectoderm, however, which resembles that of the body-wall but for the possession in parts of many nematocysts. I do not know how these conflicting statements can be reconciled, but Pax’s description is the one in accordance with what one would expect on general grounds of anemone anatomy, and it is not impossible that the curiously made-up musculature described by McMurrich is an abnormality of that particular specimen.

diomene and Stomphia. The absence of musculature on the aboral faces of the tentacles is a feature possibly foreshadowed by other Paractids in which the musculature is somewhat reduced on the outer sides of the tentacle-bases. So it seems that one must include *Ophiodiscus* in the Paractidae unless definite evidence of pseudo-tentacles should come to hand, and even then that character alone *might* not be weighty enough, as against the sum of the other characters, to place it in a separate family. Certainly it could not go to the Dendromeliidae.

Polysiphonia. Hertwig, 1882, p. 63.

Paractidae (Polysiphoniinae) with definite base. Column smooth or somewhat nodular (and in the only known species thick-walled and vase-shaped), its margin tentaculate. All the tentacles have mesogloal swellings on the outer side at the base, and their longitudinal musculature, like the radial musculature of the oral disc, is mesogloal. The oral disc is twelve-lobed though the lobes are not very deep, and the tentacles are placed at its margin in two cycles only, the number of cycles not increasing as the animal grows. The tentacles are arranged in twelve triangular groups in connection with the lobing of the disc, the twelve groups being continuous with one another. The twelve tentacles representing the primary and secondary endocœls are the largest and are placed at the points of the twelve triangles nearest the mouth, i.e. in the depressions between the disc-lobes. The other tentacles decrease in size towards the apices of the disc-lobes. The outer-cycle tentacles represent the exocœls, the inner-cycle tentacles the endocœls. The twelve oldest pairs of mesenteries are perfect and arranged in the ordinary way found in Actiniaria, and include two pairs of directives, but the other mesenteries are peculiarly arranged. In each of the exocœls between the primary and secondary pairs the younger mesenteries have a bilateral arrangement, the youngest ones appearing in the middle of the exocœl. Each of these later pairs consists of one larger and one smaller partner, and the oldest of the larger partners are perfect as well as the primary and secondary mesenteries. The primary and secondary mesenteries probably sterile, the oldest of the others fertile.

Species: *P. tuberosa*, Hertwig, 1882, p. 63. (See Carlgren, 1918, pp. 13, 36, etc.)

In 1893 McMurrich (pp. 165, 209) included *Polysiphonia* in the genus *Actinernus*, relying apparently on

the external similarity between the two. Carlgren (1918) has shown that there is no ground for fusing the two genera. The genus *Actinernus* as originally founded by Verrill has been broken up into two quite unrelated genera on anatomical grounds. The first of these is *Actinernus* proper (= *Porponia*, Hertwig), and is a member of the *Endocœlactidæ*; the second is *Actinoscypnia* and belongs to the *Actinoscypniidæ*. *Polysiphonia* is a Paractid and related to neither of them. The main differences between the three genera are as follows: *Actinernus* has its younger mesenteries developed in the *endocœls* of the older ones, and each of these younger pairs has the longitudinal muscles of its partners facing away from each other as if they were directives; in *Actinoscypnia* and *Polysiphonia* the younger mesenteries develop in the normal way, i.e. in *exocœls*, and with the longitudinal muscles of the partners facing each other. Apart from this *Actinernus* has no sphincter and the other two have a mesoglœal one. *Polysiphonia* still further differs from *Actinernus* in that its discal, radial and longitudinal tentacular musculature is mesoglœal instead of ectodermal. *Actinoscypnia* in its turn differs from *Polysiphonia* by the possession of only six pairs of perfect mesenteries instead of a larger number; by the fact that its younger mesenteries are normally developed in cycles and do not appear bilaterally in twelve special regions of growth (see above definition of *Polysiphonia*); and by having ectodermal instead of mesoglœal tentacle-and-disc muscles. It is thus seen that but for a curious superficial and external resemblance to each other the three genera are unrelated, and *Polysiphonia* remains a good genus. The curious and unusual mode of appearance of the younger mesenteries in *Polysiphonia* offers an interesting parallel to a similar mode of growth exhibited by certain *Endocœlactidæ* not related. It is probably accounted for in both cases (as Carlgren has suggested, 1918, pp. 14-15) by the facts that the oral disc is lobed and the older tentacles at least have strong basal swellings of mesoglœa, so that newly-appearing tentacles have no room for normal develop-

ment and must appear where they can, as the lobes grow, either between the bases of the lobes (*Actinernus*) or at their apices (*Polysiphonia*). Their appearing in this way carries with it the appearance of the younger mesenteries in a bilateral manner in zones related to the disc-lobes. It can hardly be the other way about (that the mesentery-development affects the tentacles), because in *Synactinernus* and *Isactinernus*, although the disc is lobed, the tentacles are small and have no basal swellings or only weak ones, and the mesenteries here develop normally in cycles. This explanation helps to elucidate the appearance of similar phenomena in unrelated forms.

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APPENDIX TO LIST OF LITERATURE.

The following list consists of references to literature which it has been neither possible nor necessary for me to consult personally, but which is mentioned in the foregoing paper in connection with some of the original descriptions of certain species listed after the generic definitions. In cases where the original description has not been consulted, one or more later and usually fuller descriptions of the species have been seen. These references are simply included for convenience in case they should be needed, and are copied from Andres, 1883, and other works. I cannot, of course, guarantee that the

descriptions referred to will be found in the works quoted, but I have done my best to select the right references.

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XII. EXPLANATION OF PLATE 22.

Illustrating Mr. T. A. Stephenson’s paper “On the Classification of Actiniaria.”

PLATE 22.

A. Piece of a mesentery. *B.* Processes of mesogloea bearing ectodermal muscle-fibres. *C.* Cilia. *D.* Diaphragm. *E.* Ectoderm. *EN.* Endoderm. *F.* Muscle-space in fig. 3; muscle-fibres in fig. 10. *H.* Small mesentery. *K.* Endodermal circular musculature. *L.* “Lip” of ectoderm. *M.* Mesogloea; in fig. 7 points to muscle in the mesogloea. *N.* Nerve-layer. *P.* Base of outer wall of a tentacle. *R.* Network of muscle-fibres and muscle-spaces in the mesogloea. *T.* Thick-walled nematocyst. *Z.* Zooxanthellæ.

Fig. 1.—Transverse section of portion of body-wall of *Sagartia miniata*, to show a cinclis. Oc. 3, obj. $1\frac{1}{2}$.

Fig. 2.—Transverse section of portion of body-wall of *S. miniata* (same specimen as that from which fig. 1 was drawn), to show a cinclis. Oc. 3, obj. $1\frac{1}{2}$.

Fig. 3.—Longitudinal section of margin of body of *S. miniata*, showing the sphincter-muscle. Oc. 3, obj. $1\frac{1}{2}$.

Fig. 4.—Transverse section of an acontium of *S. miniata*. Oc. 3, obj. $\frac{1}{6}$.

Fig. 5.—Transverse section of the diaphragm of a cinclis of *S. miniata*. Drawn with $\frac{1}{2}$ oil imm.

Fig. 6.—Longitudinal section of portion of the wall of the physa of *Peachia hastata* to show a cinclis. Oc. 3, obj. $\frac{2}{3}$.

Fig. 7.—Longitudinal section of portion of the margin of *Halcampta chrysanthellum*, showing part of the mesogloal sphincter. Oc. 3, obj. $\frac{1}{6}$.

Fig. 8.—Transverse section of a portion of the wall of a tentacle of *Stomphia churchiae*. Oc. 3, obj. $\frac{2}{3}$.

Fig. 9.—Vertical transverse section of oral disc of *Sagartia miniata*. Oc. 3, obj. $\frac{2}{3}$.